

Chapter IV: Water Column Data and Spectral Irradiance Model

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Abstract

Water samples collected monthly, for 18 months, from six sites in the Laguna Madre were analyzed to identify and quantify phytopigments using High Performance Liquid Chromatography (HPLC). In addition, water column pigment and nutrient data were acquired at 12 stations in Upper (ULM) and Lower Laguna Madre (LLM) during the summer 1996 cruise. The spatial and temporal scale of sampling provide a unique perspective on the dynamics of phytoplankton communities within the Laguna Madre. Phytopigment identification from field samples was consistent with the known pigment complex for *Aureoumbra lagunensis*, Texas brown tide. Pigment identification and pigment ratios indicate that the dominant phytoplankton at most sites was brown tide; however, other groups were also present. Extreme pigment ratios in Lower Laguna during September 1997 may be the result of a red tide bloom or a wind event suspending benthic diatoms. Additionally, this data set documents the decline of brown tide in the Upper Laguna. Nutrient data collected along a transect through the Laguna indicates that Baffin Bay and Arroyo Colorado may be sources of anthropogenic nutrients. Pigments were identified and quantified for the major seagrass species in Laguna Madre. Pigment ratios for the seagrasses were substantially higher than published values, because HPLC is more sensitive than traditional methods.

Inherent optical properties (IOPs) of Laguna Madre waters were studied in August 1997. Preliminary measurements of absorption and backscattering coefficients were performed along with analyses of total suspended solids (TSS) and pigment concentrations in both upper and lower Laguna Madre. Strong relationships were observed between IOPs and TSS, which can ultimately be used to compute spectral irradiance in the water with the radiative transfer numerical model called Hydrolight. Finally, we describe a simple spectral irradiance productivity model that can use data provided by Hydrolight to estimate algal productivity in the water column. Comparisons with standard PAR models suggest light quality is important to understanding productivity in Laguna Madre waters.

Introduction

Light attenuation occurs as a result of scattering and absorbance by water as well as suspended and dissolved materials (Kirk, 1994). Suspended solids, including phytoplankton, are responsible for the majority of light attenuation (Voss 1992). In addition to attenuation, the presence of phytoplankton pigments and dissolved organic materials e.g., humics can cause dramatic spectral shifts (Smith and Baker 1978, Yentsch 1980, Pierce et al. 1986). Laguna Madre has been disrupted by an extensive bloom of *Aureoumbra lagunensis*, Texas "brown tide" (DeYoe et al. 1997), which caused a 50% reduction in underwater light levels in some portions of the Laguna (Dunton 1994). Shading from the brown tide has resulted in the loss of seagrass from deeper portions of the Upper Laguna Madre (Onuf 1996). Although, *A. lagunensis* has been the dominant phytoplankton in some regions, other phytoplankton occur and are important in Laguna Madre.

Pigment composition is often used as a taxonomic indicator for plankton and algae. High performance Liquid Chromatography (HPLC) can detect low concentrations of pigments and can be used to identify characteristic accessory pigments. The presence and abundance of particular accessory pigments can be used to identify major taxonomic groups contributing to water column primary productivity. Thus, HPLC analysis is a sensitive tool to identify the major phytoplankton groups responsible for light attenuation and to quantify the abundance of phytoplankton. Traditional spectrophotometric analysis is limited to quantifying the relative abundance of organisms containing chlorophyll *a*.

Photosynthesis, the energy gathering mechanism of seagrasses, is primarily dependent on the availability of radiant energy and nutrients. The fluxes of these rate-limiting factors are governed by optical properties of the water column, hydrodynamic and sediment transport, and biological processes (Bidigare et al 1987). Because chlorophyll and other pigments absorb light quanta selectively from the light spectra, photosynthetic production will depend on the spectral quality of the light in the water and on the types of pigments found in the plants.

This chapter presents water column nutrient and pigment and seagrass pigment (obtained by HPLC) data collected in Upper and Lower Laguna Madre during summer 1996 cruise. Additionally, we present water column HPLC pigment data obtained at the permanent sampling stations (i.e., "Blucher platforms") from June 1996 through November 1997 and HPLC pigment data from the type culture (TBA-2) of *Aureoumbra lagunensis*. The long-term water column pigment data collected at the platforms presents a unique opportunity to examine the temporal and spatial dynamics of phytoplankton in the Laguna Madre. Included is a preliminary report produced

by R. Maffioni at the HOBI Laboratory on inherent optical properties in Laguna Madre waters based on sampling that took place in August 1997. Finally, initial testing of a spectral irradiance is included, which may lead to better estimates of seagrass production

Part I: Pigment and Nutrient Data

Sampling and Analyses

Nutrients

Water column nutrient data were acquired at 12 stations in Upper (ULM) and Lower Laguna Madre (LLM) during the summer 1996 cruise. Samples were collected in quadruplicate in 1 L acid-washed Nalgene™ bottles. After rinsing, bottles were filled three-quarters full with surface water and frozen. In the laboratory, samples were thawed and filtered. Nutrient analyses on the filtrate were conducted according to Biggs et al. (1982).

Water column pigments

Surface waters were filtered through 47 mm GF/F filters and the volume recorded (about 100 to 1000 ml). At each site and date replicate ($n = 4$) samples were obtained, filtered and subsequently analyzed. Samples were filtered under low light conditions, filters were enclosed in aluminum foil and, when possible, frozen immediately in liquid nitrogen. Filter samples were kept frozen prior to analysis. Pigments were extracted in 100% acetone and measured by High Performance Liquid Chromatography using a modification of the Mantoura and Llewellyn (1983) method. A Shimadzu diodearray detector (model SPD-M10AV) was used to detect absorbance. Absorbance peaks were then used to calculate pigment concentration ($\mu\text{g L}^{-1}$) based on extraction and sample volume. Canthaxanthin ($1 \mu\text{g ml}^{-1}$), a xanthophyll pigment not found in algae, was added to all samples and blanks as an internal standard

Seagrass pigments

Seagrass samples, *Thalassia testudinum*, *Syringodium filiforme* and *Halodule wrightii*, were extracted in the laboratory of Dr. K. Dunton, UTMSI, and an aliquot of the extract was shipped to Texas A&M for analysis. Pigments were measured by High Performance Liquid Chromatography using a modification of the method of Mantoura and Llewellyn (1983).

Laboratory pigment data

Dr. R. Greene at Texas A&M University provided samples of the Texas “brown tide” organism (clone TBA-2) for pigment analysis. Cells were grown in batch culture in f/2 media at six phosphate and ammonium concentrations at 30°C and about 100 $\mu\text{mol quanta/m}^2/\text{s}$. Pigments were extracted and measured as previously described.

Results and Discussion

Nutrients

During June 1996, nutrient concentrations were low compared to eutrophic estuaries e.g., Chesapeake Bay (Table 1). Ammonium was the most abundant form of inorganic nitrogen and its concentration ranged from 0.52 to 4.42 μM . Maxima were observed at Station 20 in the ULM and Station 25 in the LLM (Fig. 1). The former is in the vicinity of Baffin Bay, whereas the latter is in the vicinity of the Arroyo Colorado. Both of these areas are likely sources of nitrogen-rich waters, because of anthropogenic nutrient inputs. Baffin Bay, is bordered by agricultural lands treated with fertilizers and pesticides. Additionally, Baffin Bay receives several intermittent sources of freshwater, some of which are contaminated with treated wastewater. The Arroyo Colorado originates at the Harlingen wastewater treatment plant, receives effluent from shrimp farms and is the largest source of freshwater to Lower Laguna Madre. In contrast, oxidized forms of nitrogen, nitrate and nitrite, were below 0.3 μM throughout the region. Surprisingly, urea, an organic form of nitrogen, was found at high concentrations, varying from 0.2 to 3.98 μM . High abundance of urea were also documented in sediment porewater, which may have been the source for the overlying waters.

Phosphate concentrations ranged from 0.09 to 1.92 μM . Overall, the trend for phosphate appeared to be decreasing values from ULM to LLM (Fig. 2) with a significant maximum found at the same ULM region (near Baffin Bay) where the highest ammonium concentration was measured. At least during this period of the year, N:P were always lower than Redfield ratio (16:1) (Fig. 3). This suggests that additional nitrogen could lead to increased algal abundance. Finally, silicate values were never low in either portion of the Laguna (> 5 μM throughout), but decreased significantly to the west of Station 26 (Fig. 2).

Water column pigments

The HPLC analyzer was configured to detect chlorophylls *a*, *b*, *c*₁ and *c*₂ as well as 12 accessory pigments including fucoxanthin, 19' butanoyloxyfucoxanthin, diadinoxanthin, prasinoxanthin, lutein, zeaxanthin and Beta-carotene. The time series data set (Appendix 1) from the fixed stations (ULM 1-3 and LLM 1-3) represents 392 samples taken over an 18 month period. The five most prevalent pigments, besides chl *a*, were chl *c*₁*c*₂, fucoxanthin, 19' butanoyloxyfucoxanthin, diadinoxanthin and zeaxanthin. The taxonomic groups associated with the particular accessory pigments measured in the Laguna Madre is presented in Table 2. Comparisons between chlorophyll *a* measurements by HPLC and spectrophotometric methods were discussed in Chapter IV.

Table 1. Water column nutrient data for the summer 1996 cruise. Data are shown as mean concentration and standard deviation of quadruplicate samples taken at each station.

Station	Ammonium (μM)		Phosphate (μM)		Urea (μM)		Nitrate (μM)		Nitrite (μM)		Silicate (μM)	
	Conc.	Std.	Conc.	Std.	Conc.	Std.	Conc.	Std.	Conc.	Std.	Conc.	Std.
13	1.30	0.27	0.43	0.19	0.82	0.23	0.19	0.10	0.01	0.01	45.9	8.53
16	0.87	0.28	0.29	0.22	0.80	0.19	0.21	0.21	0.01	0.01	35.1	24.6
18	1.88	0.62	0.31	0.09	1.30	0.78	0.11	0.08	0.01	0.01	25.7	2.69
20	4.42	6.19	1.92	2.70	3.98	5.89	0.23	0.12	0.04	0.04	53.5	6.99
22	1.98	3.05	0.98	1.58	1.63	1.88	0.12	0.08	0.04	0.03	43.0	4.04
24	0.52	0.24	0.11	0.04	0.64	0.11	0.31	0.16	0.01	0.01	52.2	5.77
25	2.26	0.50	0.24	0.07	0.92	0.57	0.21	0.11	0.07	0.04	41.3	12.0
26	1.00	1.07	0.17	0.14	0.83	0.54	0.15	0.08	0.03	0.04	39.7	7.93
27	0.46	0.16	0.09	0.04	0.16	0.11	0.04	0.03	0.02	0.01	7.96	2.19
28	0.64	0.60	0.14	0.02	0.50	0.32	0.06	0.01	0.02	0.00	7.28	0.76
29	0.72	0.60	0.13	0.07	0.61	0.54	0.06	0.05	0.02	0.02	6.89	1.57
30	1.43	1.66	0.15	0.08	0.83	0.90	0.07	0.04	0.03	0.02	5.88	2.01

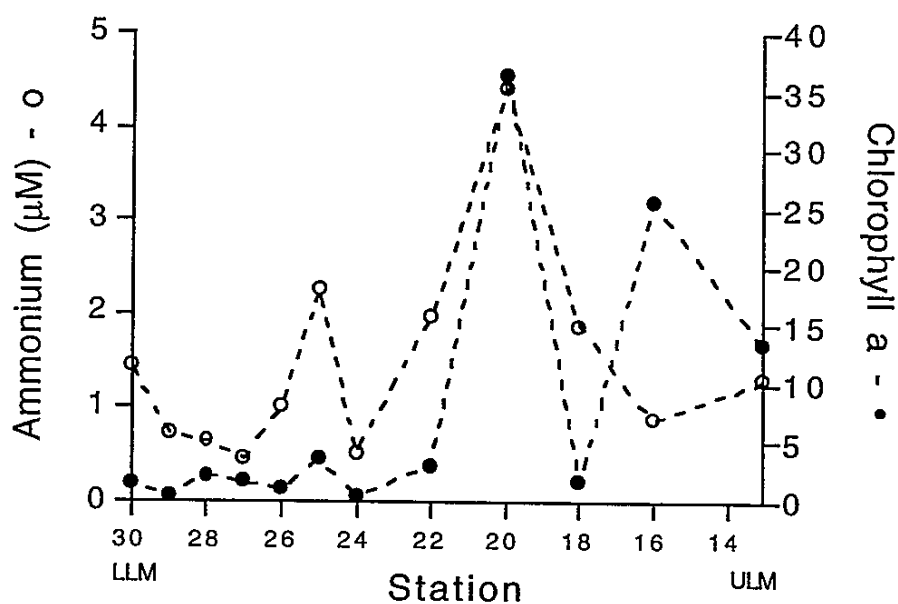


Figure 1. Ammonium (μM) and chlorophyll *a* ($\mu\text{g/l}$) concentrations along a transect through the Upper and Lower Laguna Madre during summer 1996.

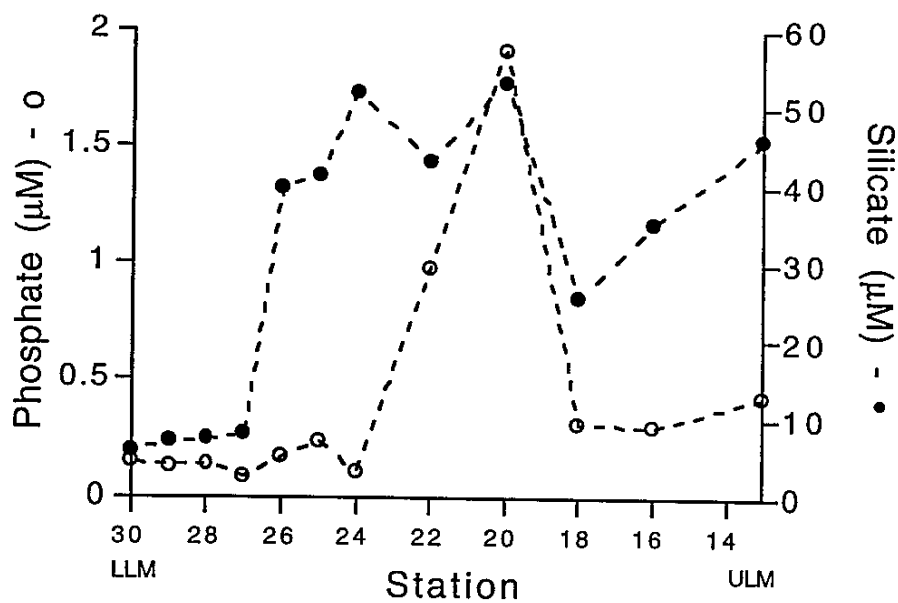


Figure 2 Phosphate (μM) and silicate (μM) concentrations along a transect through the Upper and Lower Laguna Madre during summer 1996

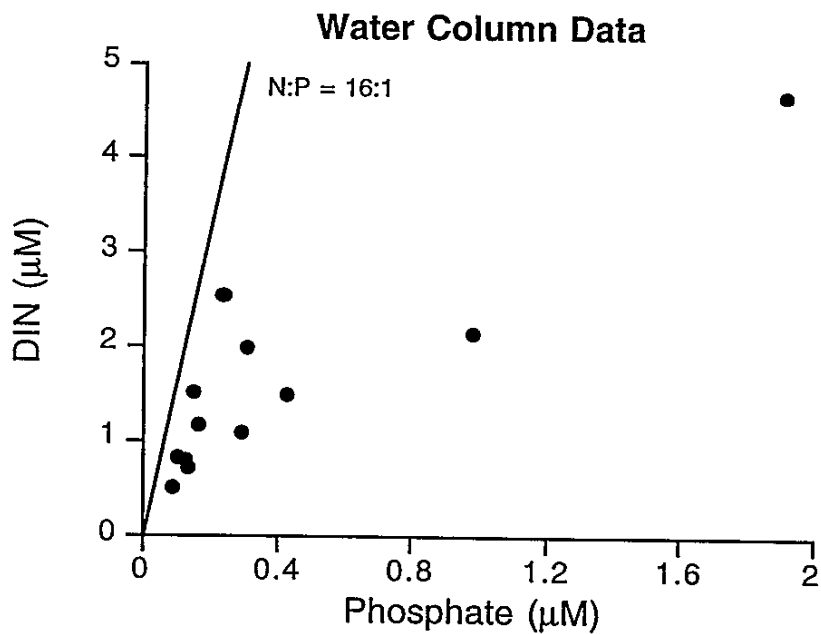


Figure 3. Dissolved inorganic nitrogen (DIN=nitrate+nitrite+ammonium; μM) versus phosphate (μM) concentrations in Upper and Lower Laguna Madre during summer 1996. Solid line represents the "Redfield Ratio"

Table 2. List of pigments observed in this study and their taxonomic-physiological significance (adapted from Bidigare 1989)

Pigment	Significance
Physiological Markers	
Chlorophyll <i>a</i>	Algal biomass and photosynthetic potential
Diadinoxanthin Zeaxanthin	Photo-protectant
Golden-brown algae	
Fucoxanthin Chlorophyll <i>c</i> ₁ , <i>c</i> ₂	Diatoms (and some chrysophytes and prymnesiophytes)
19'-butanoyloxfucoxanthin Fucoxanthin	Chrysophytes
Chlorophyll b-containing algae	
Lutein	Chlorophytes ¹
Prasinoxanthin	Prasinophytes ¹
Zeaxanthin	Prochlorophytes ¹
Phycobilin-containing algae	
Zeaxanthin	Coccoid cyanobacteria

¹also contain small amounts of zeaxanthin

During the summer 1996 cruise, chl *a* values ranged from 0.43 to 25.60 µg/l. Chlorophyll *a* values during the summer 1996 cruise were higher in the ULM compared with the LLM (Fig. 1, Table 3), and while there was no obvious correlation with nutrient abundance, concentrations of both were higher in the ULM (Figs 2 & 3).

Contour plots provide a unique perspective on the spatial and temporal dynamics of pigment concentrations in Laguna Madre. As expected the pigment composition changed as a function of both location and time (Figs. 4 through 9). Chlorophyll *a* values were high at all sampling locations during winter and spring 1997 (Fig. 4). At LLM2, which typically has very low chlorophyll levels (e.g. <3 µg L⁻¹), chl *a* values were around 10 µg L⁻¹ from April to June and elevated concentrations persisted until September 1997 (Fig. 4). Elevated levels (> 2.5 µg L⁻¹) of fucoxanthin occurred at most sites between February and May 1997. High fucoxanthin concentrations (i.e., 10 µg L⁻¹) correspond with chlorophyll *a* values in excess of 30 µg L⁻¹ (Fig. 4

and 5) Elevated chl c_1c_2 concentrations also occurred at most sites between February and May and the highest concentrations ($0.5 \mu\text{g L}^{-1}$) coincide with chlorophyll a values in excess of $30 \mu\text{g L}^{-1}$ (Fig. 4 and 6). The pigments diadinoxanthin, zeaxanthin and 19' butanoyloxyfucoxanthin (Figs. 7, 8 and 9) also exhibited maxima that coincided with high chl a concentrations (Fig. 4). All of these accessory pigments are components of the light harvesting complex associated with the Texas "brown tide" *Aureocoumbra lagunensis* (DeYoe et al. 1997). Bidigare (1989) reported that *Aureococcus anophagefferens*, New England "brown tide", had significant amounts of fucoxanthin, chlorophyll c , 19'-butyloxofucoxanthin, and a small quantity of diadinoxanthin.

Although *A. lagunensis* was the dominant phytoplankton during the spring other phytoplankton were present and important contributors to primary production. The presence of diatoms is indicated by the combination of fucoxanthin and chlorophyll c_1c_2 . Both of these pigments were observed in most samples, and the presence of diatoms would be consistent with the concentrations of silicate in these waters (Fig. 2). The other pigments, lutein, zeaxanthin and prasinoxanthin, suggest the presence of chlorophytes, prasinophytes and cyanobacteria, respectively (Table 2). It must be stated that this type of information can also be obtained, and with more detail, from microscopy counts. However, our main reason for measuring pigment composition was our interest in modeling radiative transfer of light in the Laguna water column (see Preliminary Spectral Irradiance Model Section).

The ratio of accessory pigments to chlorophyll a in a sample provides a technique to examine the relative contribution of various algal groups. Particular algal groups often have characteristic pigment ratios. For example, DeYoe et al. (1997) used pigment ratios, in part, to delineate between *A. anophagefferens*, *A. lagunensis* and *P. calceolata*, which are all members of the class Pelagophyceae. *A. lagunensis* characteristically has chl c : chl a ratio of 0.1, a fucoxanthin : chl a ratio of about 0.3 and a diadinoxanthin: chl a ratio around 0.1 (DeYoe et al. 1997). Using these values as a guideline, *A. lagunensis* appears to be the dominant phytoplankton at all of the sampling stations, with a few notable exceptions (Figs. 10 through 15). At LLM 1 during September 1997, the fucoxanthin:chl a and the diadinoxanthin:chl a values were about 6.0, which are indicative of either diatoms or dinoflagellates. These extreme pigment ratios may have been related to the red tide bloom (*Gymnodinium breve*) that occurred at about the same time or to a wind event suspending benthic diatoms. The first winter fronts i.e., wind events generally occur during late September (Brown and Kraus 1997).

Table 3 Water column HPLC pigment data for the summer 1996 cruise. Data are shown as mean concentration and standard deviation of quadruplicate samples taken at each station. The "brown tide" station was taken in upper Laguna Madre during a "brown tide" bloom. Abbreviations B.D. = below detection; 19-But = 19-butanoyloxyfucoxanthin.

Station	Date	Chlorophyll a ($\mu\text{g g}^{-1}$)		Chlorophyll c ($\mu\text{g g}^{-1}$)		Chlorophyll b ($\mu\text{g g}^{-1}$)		Lutein ($\mu\text{g g}^{-1}$)	
		Conc.	Std.	Conc.	Std.	Conc.	Std.	Conc.	Std.
13	6/1/96	13.41	1.36	2.00	0.03	B.D.	B.D.	0.43	0.12
16	6/1/96	25.60	1.77	1.99	0.17	1.85	0.20	B.D.	B.D.
18	6/1/96	1.65	0.04	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.
20	6/1/96	36.35	2.44	2.06	0.44	B.D.	B.D.	B.D.	B.D.
22	6/1/96	3.08	0.25	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.
24	6/1/96	0.43	0.11	B.D.	B.D.	B.D.	B.D.	0.17	0.01
25	6/1/96	3.68	0.53	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.
26	6/1/96	1.06	0.10	B.D.	B.D.	B.D.	B.D.	0.11	0.02
27	6/1/96	1.66	0.06	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.
28	6/1/96	2.23	0.05	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.
29	6/1/96	0.46	0.04	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.
30	6/1/96	1.60	0.07	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.
"Brown Tide"	6/29/96	35.28	0.00	3.61	0.00	0.83	0.00	0.30	B.D.

Table 3 Continued.

Station	Date	Fucoxanthin ($\mu\text{g g}^{-1}$)		Zeaxanthin ($\mu\text{g g}^{-1}$)		Diadinoxanthin ($\mu\text{g g}^{-1}$)		19-But ($\mu\text{g g}^{-1}$)		Prasinoxanthin ($\mu\text{g g}^{-1}$)	
		Conc.	Std.	Conc.	Std.	Conc.	Std.	Conc.	Std.	Conc.	Std.
13	6/1/96	1.55	0.05	0.65	0.05	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.
16	6/1/96	0.93	0.04	1.21	0.39	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.
18	6/1/96	0.60	0.08	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.
20	6/1/96	6.18	0.58	1.39	0.10	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.
22	6/1/96	0.66	0.07	0.21	0.01	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.
24	6/1/96	0.13	0.08	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.
25	6/1/96	1.08	0.12	0.15	0.05	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.
26	6/1/96	0.27	0.60	B.D.	0.00	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.
27	6/1/96	0.30	0.04	0.10	0.00	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.
28	6/1/96	0.85	0.04	0.28	0.01	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.
29	6/1/96	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.
30	6/1/96	0.06	0.02	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.
Brown Tide	6/29/96	10.59	0.00	0.42	B.D.	2.41	B.D.	6.11	B.D.	0.17	B.D.

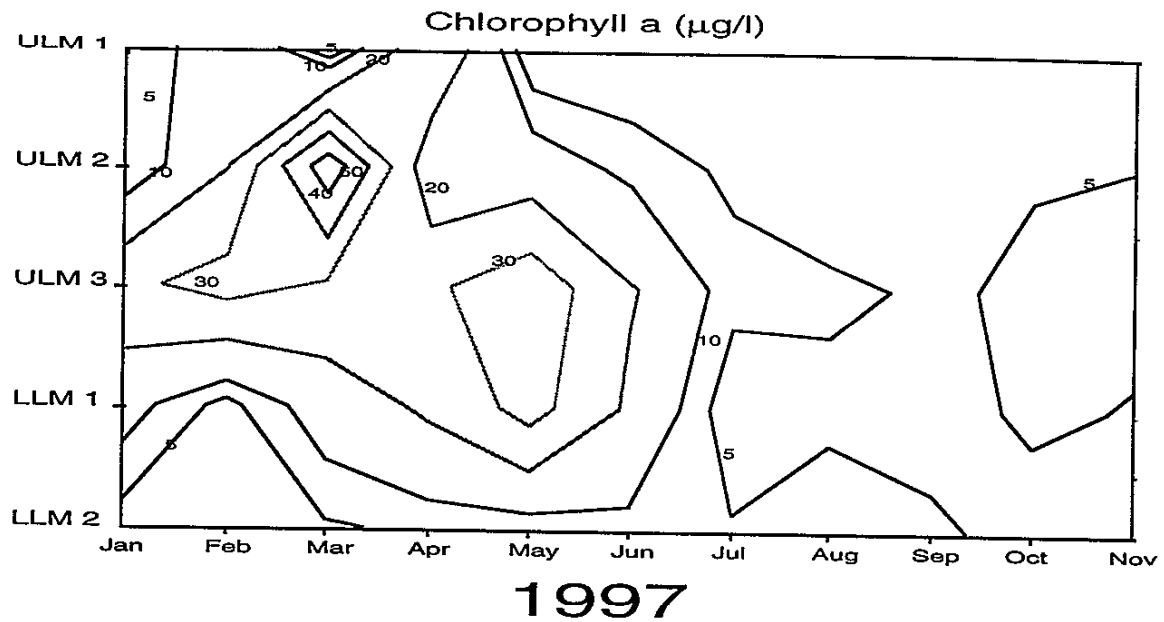


Figure 4. Contour plot of chlorophyll *a* concentration at the fixed sampling stations in Laguna Madre from North (ULM1) to South (LLM2) during the period January to November 1997.

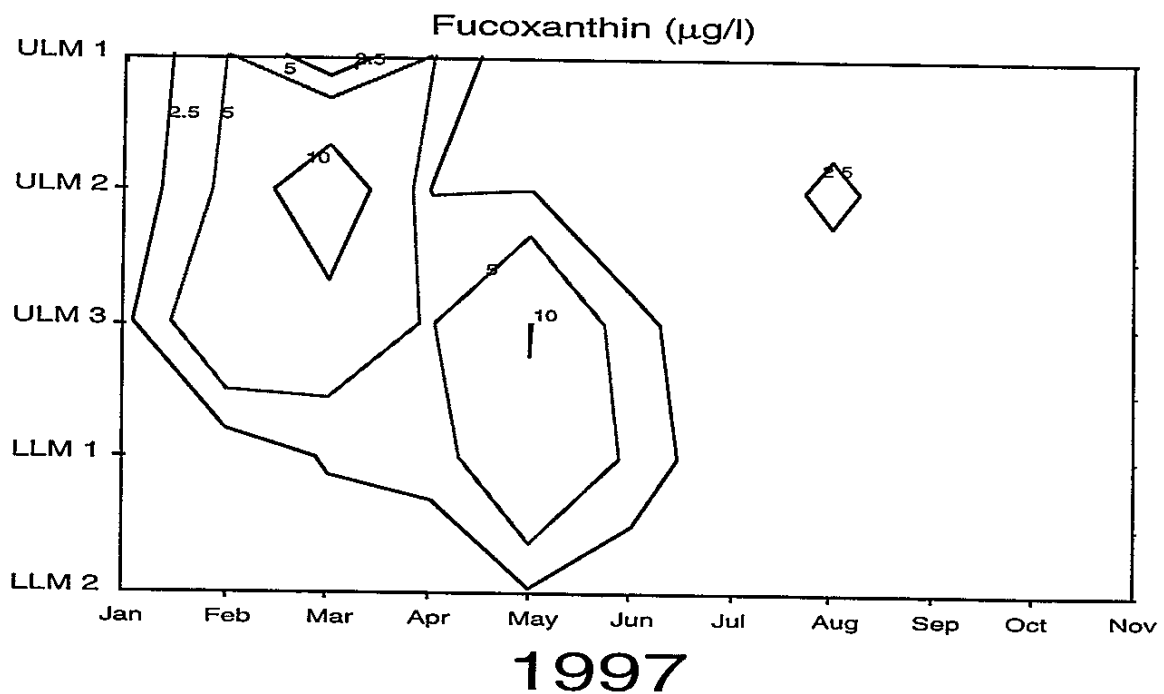


Figure 5. Countour plot of fucoxanthin concentration at the fixed sampling stations in Laguna Madre (from North to South) during the period January to November 1997.

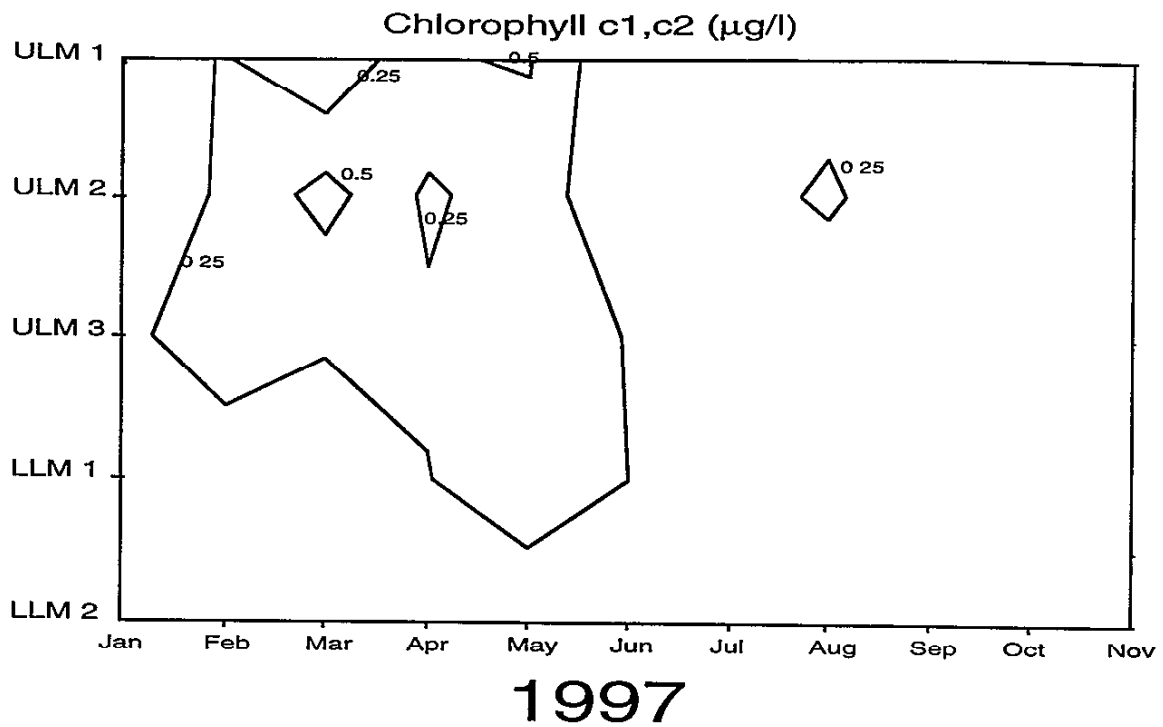


Figure 6. Countour plot of chlorophylls c_1 and c_2 concentration at the fixed sampling stations in Laguna Madre (from North to South) during the period January to November 1997.

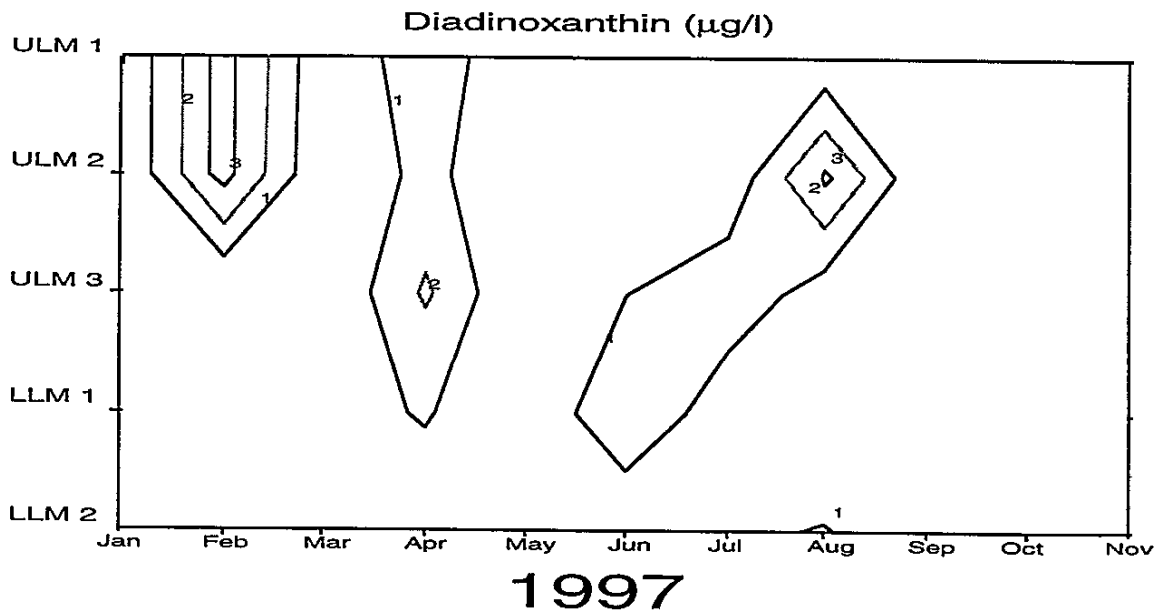


Figure 7. Countour plot of diadinoxanthin concentration at the fixed sampling stations in Laguna Madre (from North to South) during the period January to November 1997

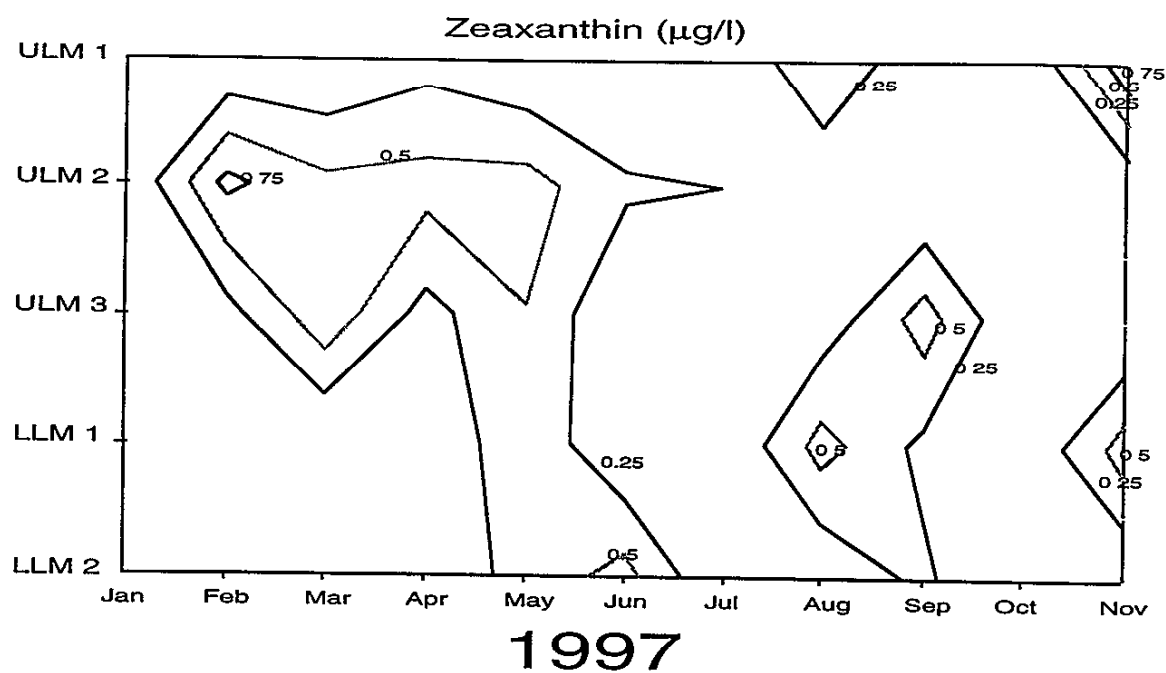


Figure 8 Countour plot of zeaxanthin concentration at the fixed sampling stations in Laguna Madre (from North to South) during the period January to November 1997.

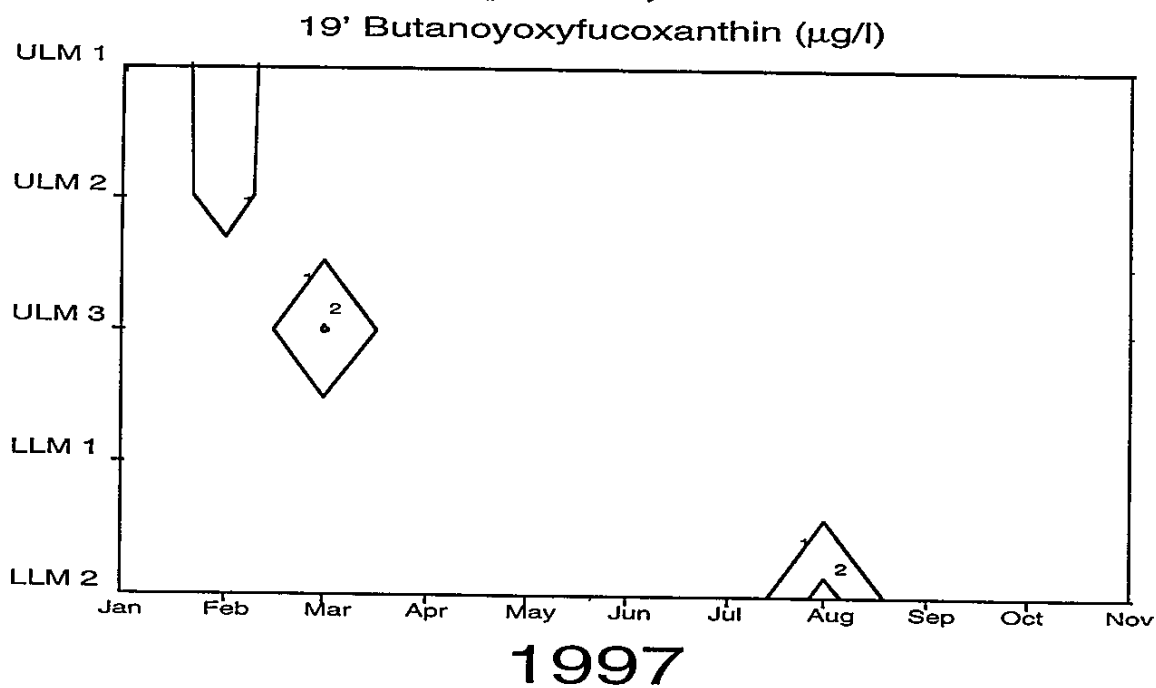


Figure 9. Countour plot of 19' butanoyloxyfucoxanthin concentration at the fixed sampling stations in Laguna Madre (from North to South) during the period January to November 1997.

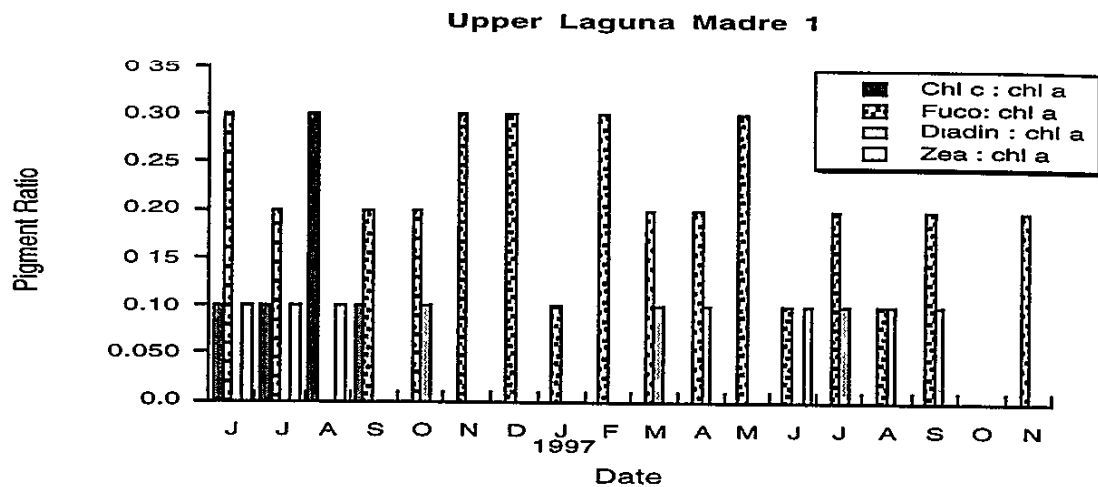


Figure 10 Pigment ratios for the most prevalent pigments relative to chl *a* at station ULM1 (Corpus Christi Bay) from June 1996 to November 1997. Missing data points are a result of pigment concentrations below the detection limit of HPLC.

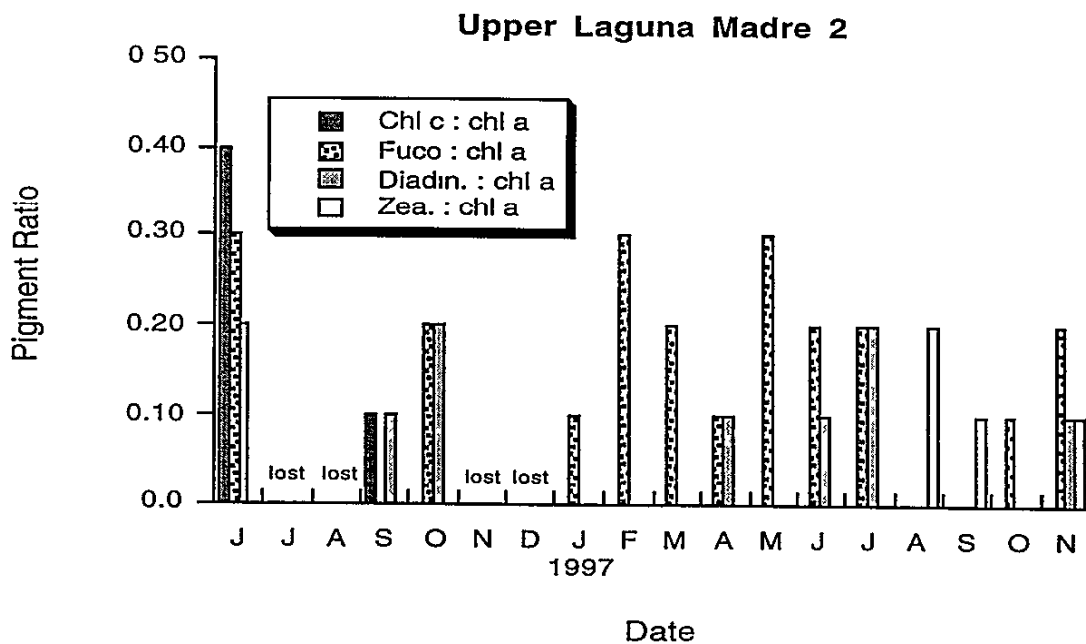


Figure 11 Pigment ratios for the most prevalent pigments relative to chl *a* at station ULM2 (South of Bird Island Basin) from June 1996 to November 1997. Missing data points are a result of pigment concentrations below the detection limit of HPLC.

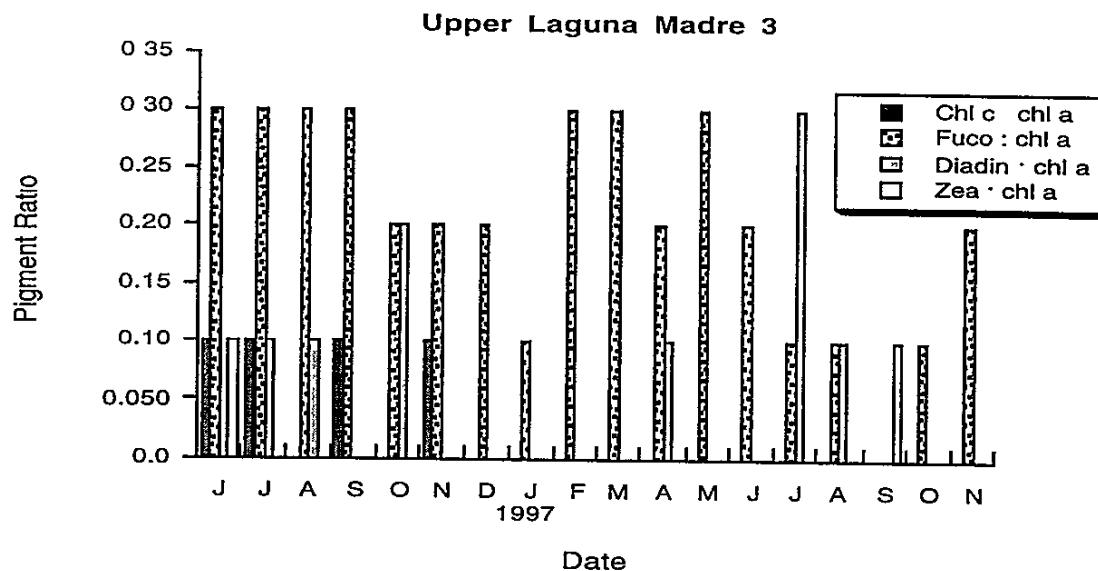


Figure 12. Pigment ratios for the most prevalent pigments relative to chl *a* at station ULM3 (North of the Land Cut) from June 1996 to November 1997. Missing data points are a result of pigment concentrations below the detection limit of HPLC

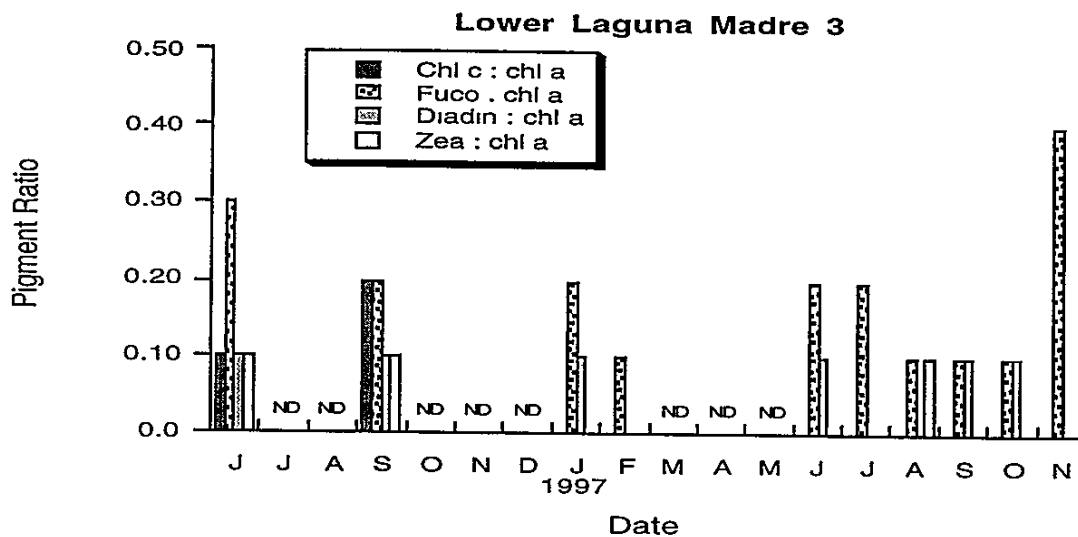


Figure 13. Pigment ratios for the most prevalent pigments relative to chl *a* at station LLM3(near Port Mansfield) from June 1996 to November 1997.

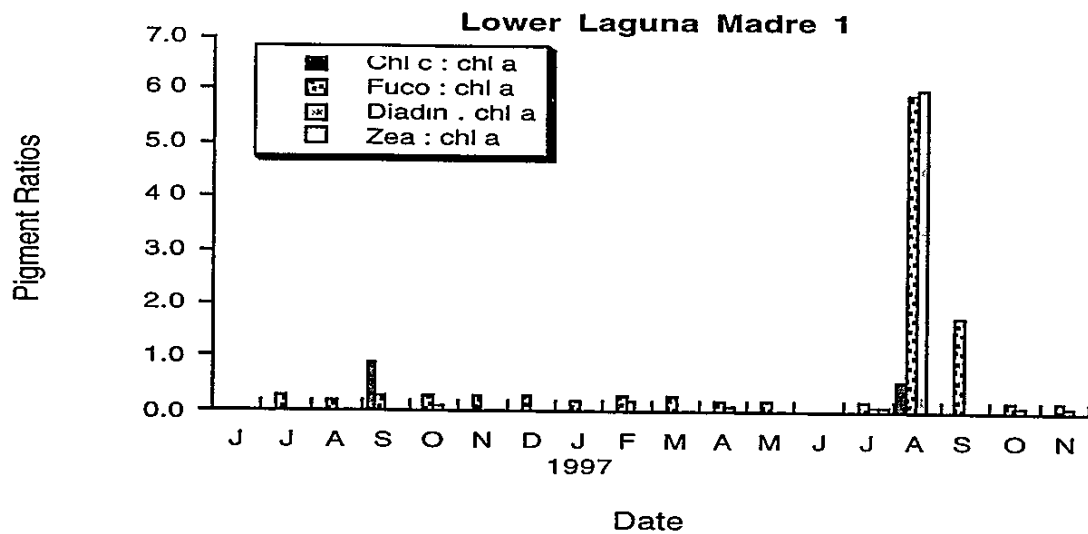


Figure 14. Pigment ratios for the most prevalent pigments relative to chl *a* at station LLM1(dredged material placement area 233) from June 1996 to November 1997. Missing data points are a result of pigment concentrations below the detection limit of HPLC.

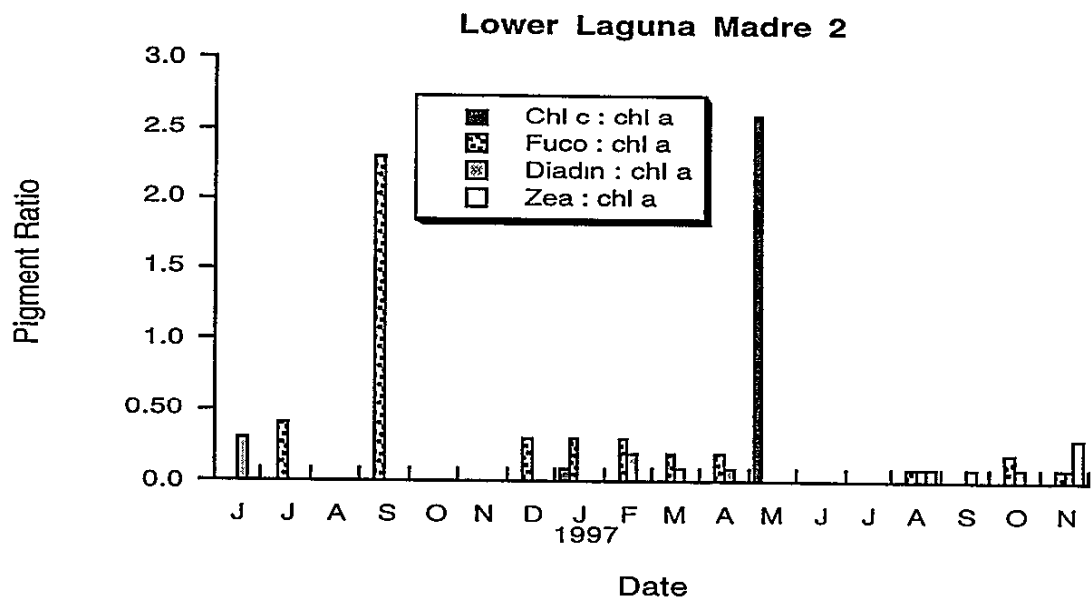


Figure 15. Pigment ratios for the most prevalent pigments relative to chl *a* at station LLM2 (seagrass bed near South Padre Island Convention Center) from June 1996 to November 1997. Missing data points are a result of pigment concentrations below the detection limit of HPLC

Seagrass pigments

Concentrations of chlorophyll *a*, chlorophyll *b* and lutein are shown for seagrasses in Table 4. Stations 13-20 were characterized by *Halodule wrightii*, stations 22-26 were dominated by *Syringodium filiforme* and stations 27-30 were dominated by *Thalassia testudinum*. Ratios of chlorophyll *b* to chlorophyll *a* varied from 0.51 to 0.80, but did not seem to vary with location in the Laguna. Although an order of magnitude smaller, .049 to .080, the range of values was similar for lutein to chlorophyll *a* ratios. Chlorophyll *b* to chlorophyll *a* ratios can be used as an indicator of light stress in seagrasses. High chl *b:a* ratios indicate that the plants have invested energy in an accessory pigment (i.e., chl *b*) in an attempt to maximize the light harvesting potential of the chloroplast. The chl *b:a* ratios calculated using spectrophotometric data, ranging between 0.3 and 0.5 (Czerny and Dunton 1995, Lee and Dunton 1996) were substantially lower than values calculated using HPLC methods (Table 4). This discrepancy is probably a result of the HPLC method's extreme sensitivity and resolution.

Table 4 Seagrass HPLC pigment data for the summer 1996 cruise. Data are shown as mean concentration and standard deviation of quadruplicate samples taken at each station. See text for description of dominant seagrasses at each site. Also included are the ratios of chlorophyll *b* to chlorophyll *a* (Chl*b*/Chl*a*) and lutein to chlorophyll *a* (Lutein/Chl*a*). A potential outlier is shown in bold type.

Station	Species	Chlorophyll <i>a</i> ($\mu\text{g g}^{-1}$)		Chlorophyll <i>b</i> ($\mu\text{g g}^{-1}$)		Lutein ($\mu\text{g g}^{-1}$)		Chl <i>b</i> / Chl <i>a</i>	Lutein/ Chl <i>a</i>
		Conc.	Std.	Conc.	Std.	Conc.	Std.		
13	<i>Hw</i>	1804	140.1	915.6	53.38	95.30	25.22	0.51	0.053
16	<i>Hw</i>	1496	353.0	1107	748.7	92.96	23.82	0.74	0.062
18	<i>Hw</i>	1865	690.7	3009	3743	106.6	39.10	1.61	0.057
20	<i>Hw</i>	2126	439.4	1092	263.6	118.2	26.43	0.51	0.056
22	<i>Sf</i>	250.7	64.78	179.4	46.76	20.16	5.079	0.72	0.080
24	<i>Sf</i>	460.5	90.04	289.5	49.38	36.30	6.193	0.63	0.079
25	<i>Sf</i>	742.2	323.5	476.3	200.8	51.74	20.42	0.64	0.070
26	<i>Sf</i>	602.1	370.2	394.6	150.4	40.56	16.00	0.66	0.067
27	<i>Tt</i>	484.3	301.5	389.2	457.1	29.65	13.05	0.80	0.061
28	<i>Tt</i>	496.3	97.73	320.5	283.2	24.56	4.174	0.65	0.049
29	<i>Tt</i>	734.0	173.3	501.7	405.8	38.13	10.44	0.68	0.052
30	<i>Tt</i>	663.2	129.8	430.9	299.3	37.22	9.204	0.65	0.056

Laboratory pigment data

As mentioned earlier, Bidigare (1989) reported on the pigment composition of an *Aureococcus anophagefferens* culture (New England "brown tide") obtained from E.M. Cosper at SUNY, Stony Brook. We measured the pigment composition of a sample taken during a "brown tide" bloom in the ULM on 29 June 1996, and the type clone (TBA-2) of Texas "brown tide". Samples of TBA-2 were obtained from Dr. Richard Greene at Texas A&M University. Comparison of preliminary results are shown in Table 5. These preliminary data indicate significant differences in

pigment composition between field and laboratory samples of *A. lagunensis*. However, recent more thorough work, has shown a greater similarity in pigment ratios between cultured (TBA-2) and field samples of Texas “brown tide” (DeYoe et al 1997). Furthermore, ribosomal RNA sequencing indicates that *A. anophagefferens* and *A. lagunensis* are distinct genera and species but both are distant relatives of *Pelagomonas calceolata* (DeYoe et al. 1995). The pigment composition of the Texas “brown tide” alga can be used in the spectral irradiance model to better described light attenuation in the Laguna Madre.

Table 5 HPLC pigment data for “brown tide” alga. Data for *Aureococcus anophagefferens* are from Bidigare (1989). Abbreviations: a=chlorophyll a, c=chlorophyll c_1, c_2 ; bf=19'-butanoyloxyfucoxanthin; f=fucoxanthin; dn=diadinoxanthin, z=zeaxanthin; B.D.=below detection.

Sample	c:a	bf:a	f:a	dn:a	z:a
<i>Aureococcus anophagefferens</i>	0.42	0.21	0.54	0.05	B.D.
Bidigare (1989)					
Texas “brown tide” (clone TBA-2)	B.D.	B.D.	0.31	0.31	0.06
Sample from “brown tide” bloom	0.10	0.17	0.30	0.07	0.01

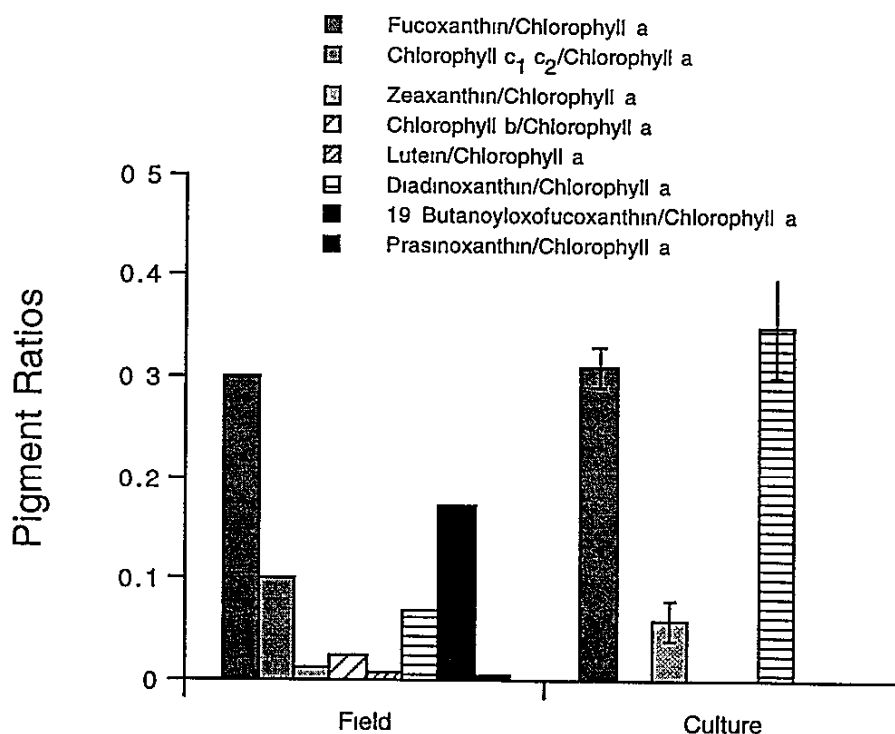


Fig. 16. Comparison of pigment ratios for *Aureocoumbra lagunensis* sample taken in Upper Laguna Madre during a “brown tide” bloom and the isotype culture (TBA-2)

Part II: Preliminary Optical Property Data

Overview

Following is a preliminary summary and analysis of the Laguna Madre experiment conducted in August 1997. Overall, there appears to be very good correlation between scattering and TSS. In analyzing the data sets, I had to make some assumptions. Otherwise, they may be due to measurement errors or real outliers due to actual variability. Correlation with absorption was not very good. Since the absorption properties of suspended sediments has yet to be definitively characterized in the literature, our findings may indeed be real. But there is also the strong possibility that the absorption values as determined by the AC9 contain significant errors. This would not be surprising given the well-known problems with the accuracy of the absorption by suspended sediments.

The PRR600 data have been reduced, but I have not yet analyzed the results. Recall that the PRR600 measures the spectral irradiance and radiance at six wavelengths, in addition to PAR. In reducing the data, I checked the numbers and all the data look quite reasonable, so I am confident that we have an excellent radiometric data set. This will be important for closure in comparing the light field measurements with the inherent optical property measurements. Ultimate closure will be achieved when we compare these measured results with the radiative transfer calculations using Hydrolight. The Hydrolight calculations are the simplest part of this study, but it is also the last part after all the measurements are properly processed.

Overall it is my evaluation that we have an excellent data set for both the Army Corps report and at certainly one or two seminal papers on this topic. Most important, we will need to add to the existing TSS and IOP measurements with emphasis on determining the errors associated with TSS measurements. It is the TSS that is central to the correlation with the optical measurements, and the parameterization of IOP's with TSS is one of the most unique and important aspects of this work.

AC9 Measurements

The AC9 measures the volume absorption and beam attenuation coefficients, denoted a and c , respectively, at nine wavelengths, where wavelength is denoted by λ . The nine wavelengths are: 412, 440, 488, 510, 532, 589, 620, 676, 715 nm. Because the AC9 is a flow-through, pumped system, a time series of a and c was measured at each station and the average values computed over a segment of each series. Examples of the spectra of a and c are shown in Figs 17 and 18. Note that both a and c yield exponential curves as a function of λ . This was consistent throughout all of

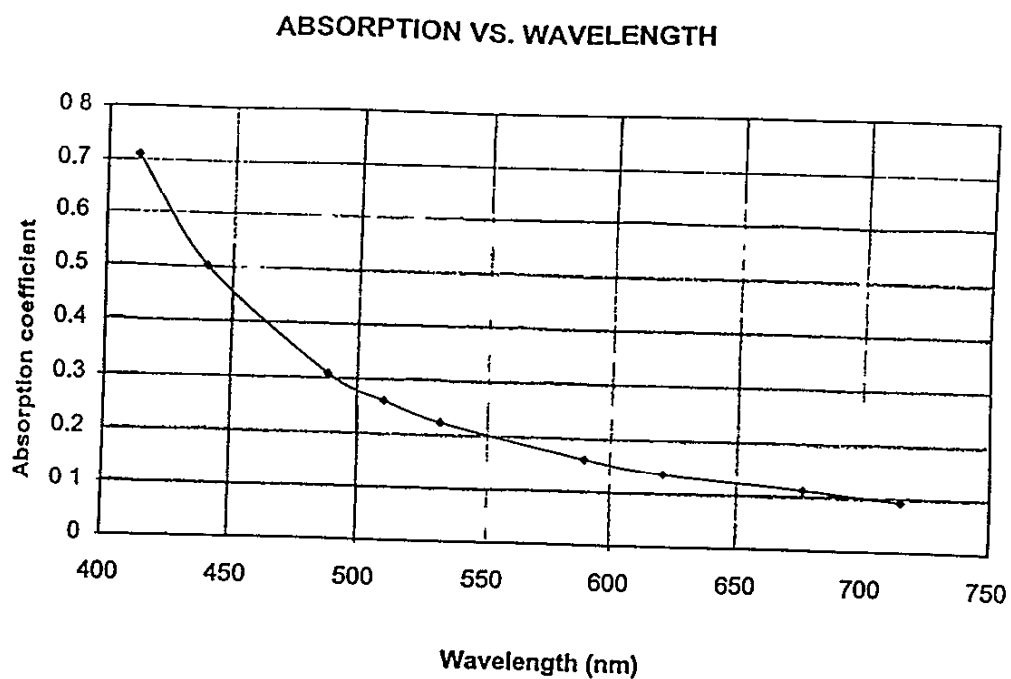


Fig 17. Absorption coefficient versus wavelength

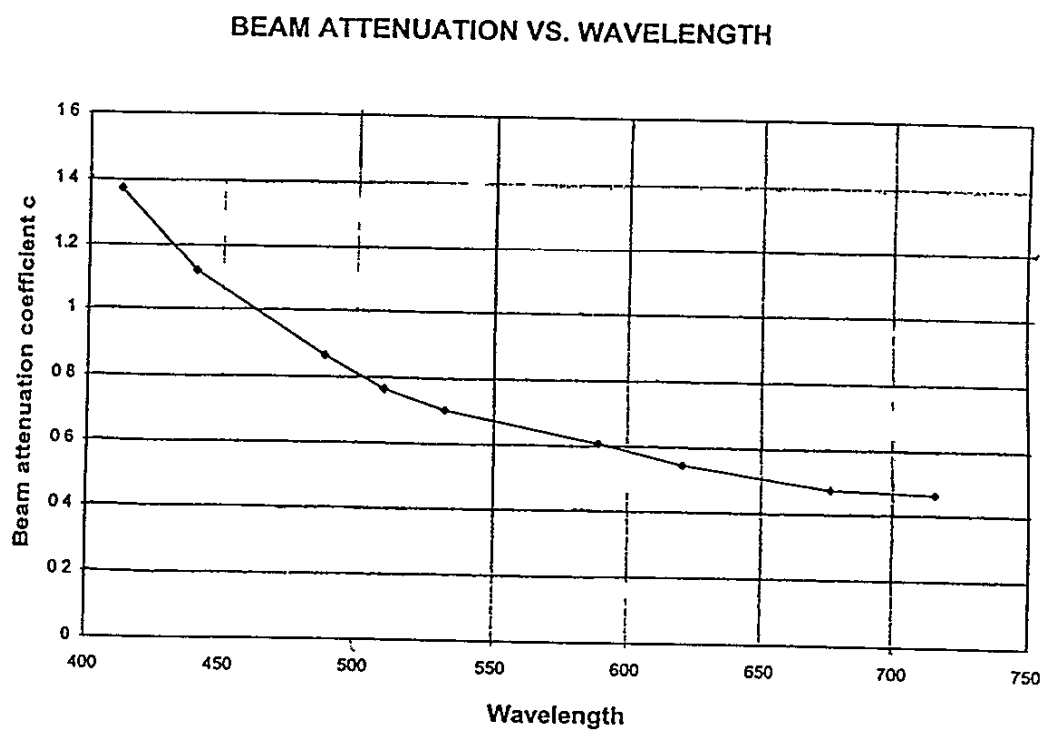


Fig 18. Beam attenuation coefficient versus wavelength.

the data sets and indicates that the dominant influence on the inherent optical properties (IOP's) is the total suspended solids (TSS), presumed to be primarily inorganic resuspended sediments

For the purposes of modeling, we will parameterize the absorption coefficient $a(l)$ and the total scattering coefficient $b(l) = c(l) - a(l)$ with exponentials of the form

$$a(\lambda) = a(\lambda_0) \exp[-\gamma_a(\lambda - \lambda_0)], \quad (\text{EQ 1})$$

$$b(\lambda) = b(\lambda_0) \exp[-\gamma_b(\lambda - \lambda_0)], \quad (\text{EQ 2})$$

where $\lambda_0 = 412 \text{ nm}$ is the reference wavelength and γ_a, γ_b are exponential coefficients for absorption and scattering. Note that, in general, γ_a, γ_b are functions of the type of sediment. For Laguna Madre, we assume that these coefficients are constant. Preliminary analysis of the data indicates that this is a good assumption.

The total scattering coefficient b is used instead of the beam attenuation coefficient c because b is a more fundamental optical property. Although c is measured directly with the AC9, it is a derivative optical quantity from a and b , namely $c = a + b$. It is the absorption and scattering properties of the suspended sediments, as characterized by a and b , that we wish to determine.

PRR Measurements

The PRR600 measures the spectral irradiance E_d at six wavelengths, plus PAR (photosynthetically available radiation), and the spectral radiance L_u at six wavelengths. The wavelengths are 380, 412, 443, 490, 510, 555. In addition to the in-water radiometric measurements made with the PRR600, the downwelling spectral irradiance onto the surface of the water was measured with a surface radiometer. At most of the sites, these radiometric measurements were made at two

depths. Measurements of E_d at two depths yields the downwelling diffuse attenuation coefficient, K_d . The relationship between $E_d(z)$, where z is the depth, and K_d is given by

$$E_d(z_2) = E_d(z_1) \exp[-K_d(z_2 - z_1)] \quad (\text{EQ 3})$$

assuming Beer's law. In this coordinate system, z is positive downward so the $z_2 > z_1$

From these measurements and computations of K_d , which, it should be noted, is a function of I , the solar irradiance incident on the bottom, or more importantly on a seagrass canopy, can be computed. One objective then is to relate $K_d(I)$ to the TSS. Once K_d can be estimated or modeled for a given amount of resuspended sediments as quantified by TSS, the downwelling spectral irradiance incident on the bottom or a seagrass canopy can be computed.

Example spectra of $E_d(I)$ measured at Laguna Madre with the PRR 600 are shown in Figs. 19 and 20. Figure 19 shows the results of a relatively low concentration on TSS at a depth of 0.77 m and Figure 20 shows the results at a relatively high concentration at a slightly shallower depth of 0.5 m. Note not only the significantly lower values of E_d at the higher TSS concentrations, as expected, but also the change in the spectral curve in going from low to high concentrations of TSS. This effect is a result of exponential dependence of a , and especially b , on wavelength for inorganic resuspended sediments, as we found in Laguna Madre.

TSS Measurements

Total suspended solids were determined from bottle samples, which were taken directly from the water flowing through the AC9. The sample was filtered in duplicate and the averages are shown in Table 6. These averages were used in correlating TSS with a , b , and c .

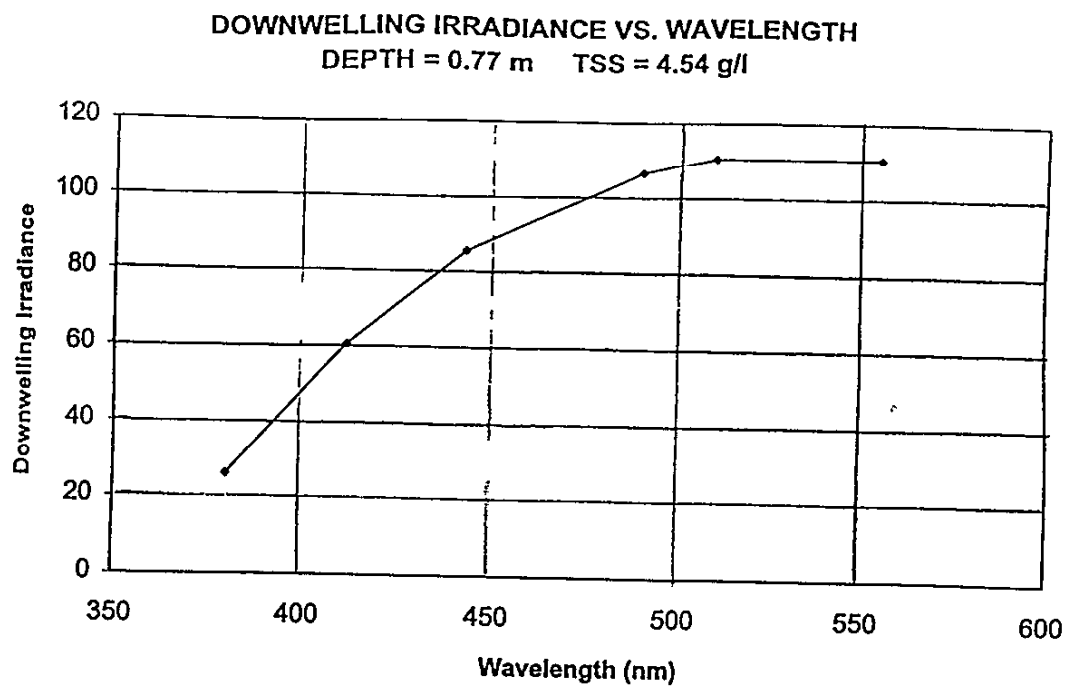


Fig 19. Downwelling irradiance versus wavelength for TSS = 4.54 mg/l at a depth of 0.77 m.

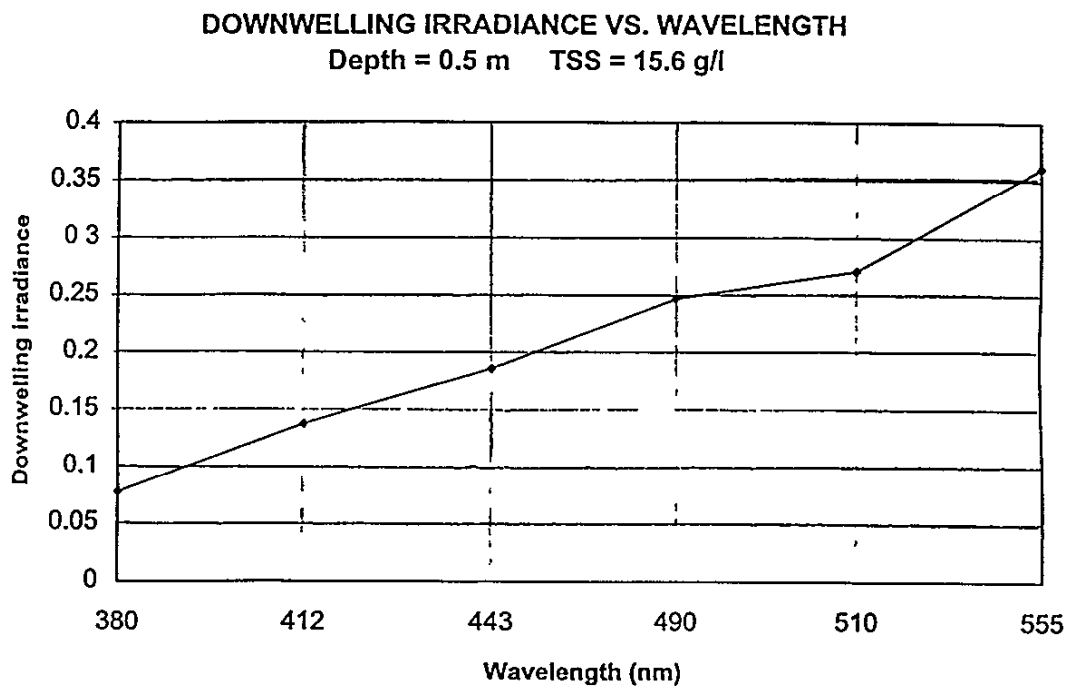


Fig 20. Downwelling irradiance versus wavelength for TSS = 15.6 mg/l at a depth of 0.5 m.

AC9 versus TSS

To see how well the inherent optical properties (IOP's) correlated with TSS for the entire data set collected at Laguna Madre, we plotted c , a , and $b = c - a$, versus TSS for the entire TSS data set. Figs. 21 and 22 show beam attenuation at 412 and 440 nm, respectively versus TSS. Note the surprisingly good correlation of c with TSS over the entire data set, including all locations and times at Laguna Madre. It is hoped that the few outliers can be better understood, and perhaps reasonably excluded, when a more detailed study of the accuracy of the method in the field is concluded. If these outliers are considered to be accurate measurements, the perhaps they can be associated with anomalous field conditions.

Figures 23 and 24 show absorption at the same two wavelengths (412,440) versus TSS. Clearly the correlation is not nearly as good as with beam attenuation. It is possible that the scatter in the absorption versus TSS correlation is due to measurement errors in the absorption coefficient. The absorption is measured by the AC9 is known to contain errors due to scattering. To some degree this error can be corrected, and was corrected in the data shown here. However, the scattering error cannot be removed completely. Nonetheless, due to the systematic nature of the scattering error, it is unlikely that most of the "scatter" in the plot of a versus TSS is due only, or even primarily, to the errors in the absorption measurement. There is a strong possibility that the absorption contained significant contributions from colored dissolved organic matter (CDOM) that was to some degree uncorrelated with the scattering caused by the suspended solids. Also, absorption by suspended sediments is not well known or characterized, and our results may simply reflect the natural variability in absorption by these inorganic particles.

In Laguna Madre (excluding brown tide), it is clearly suspended solids, primarily inorganic, that have the largest effect on the water optical properties. These suspended sediment particles scatter much more than they absorb light (although the scattering does "enhance" the absorption via optical pathlength increase). It is to be expected that the magnitude of scattering increases in proportion to particle concentration. Thus, of the optical properties a , b , and c , we should expect b to yield the greatest correlation with TSS. Figures 25 and 26 show the total scattering coefficient b versus TSS for the entire data set. As with the beam attenuation coefficient c , the total scattering coefficient b shows a high correlation with TSS. This is to be expected since the largest contribution to c comes from b (recall that $c=(a+b)$). More importantly, b , unlike c , does not

BEAM ATTENUATION VS. TSS

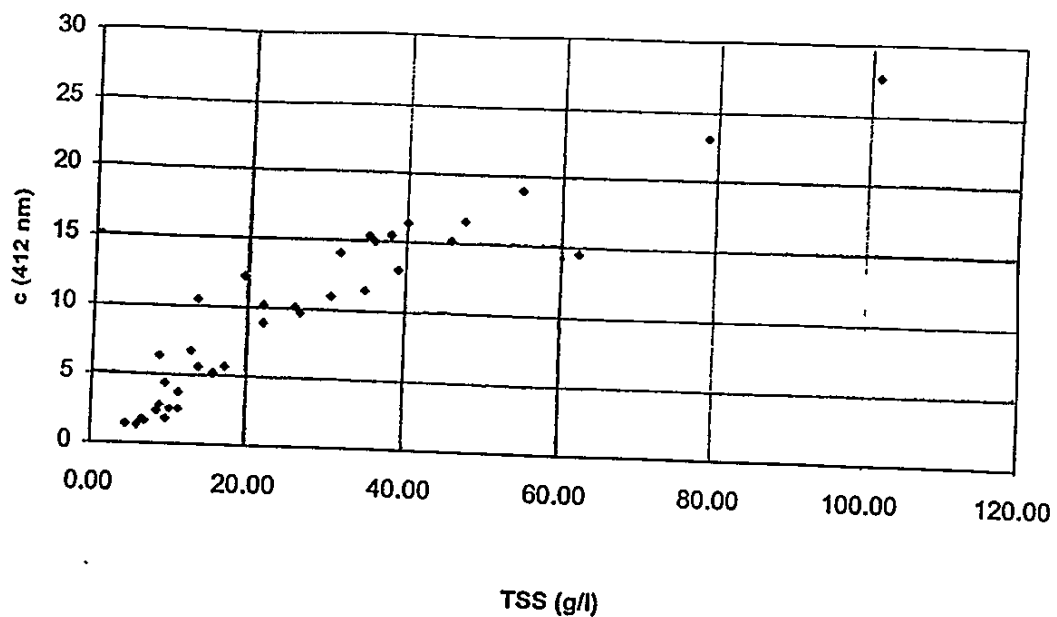


Fig 21. Beam attenuation coefficient versus TSS at a wavelength of 412 nm.

BEAM ATTENUATION VS. TSS

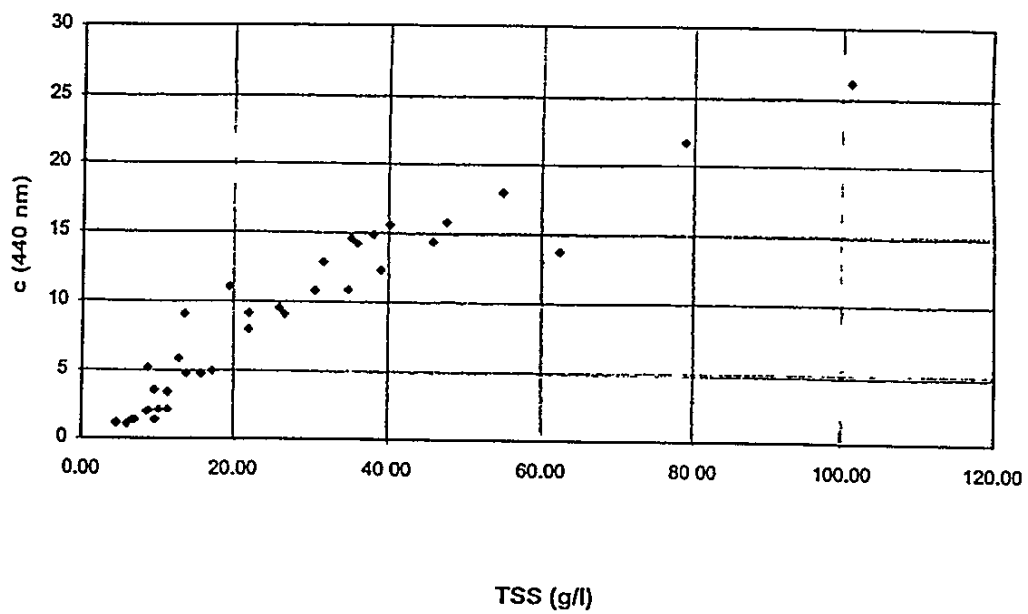


Fig 22. Beam attenuation coefficient versus TSS at a wavelength of 440 nm

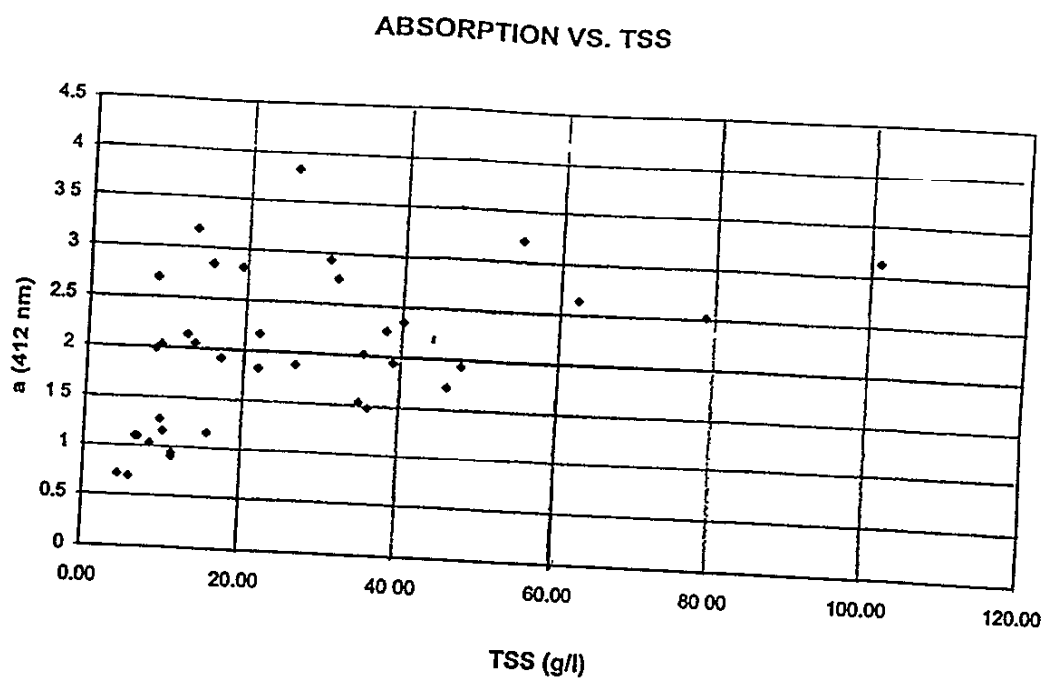


Fig 23. Absorption versus TSS at a wavelength of 412 nm

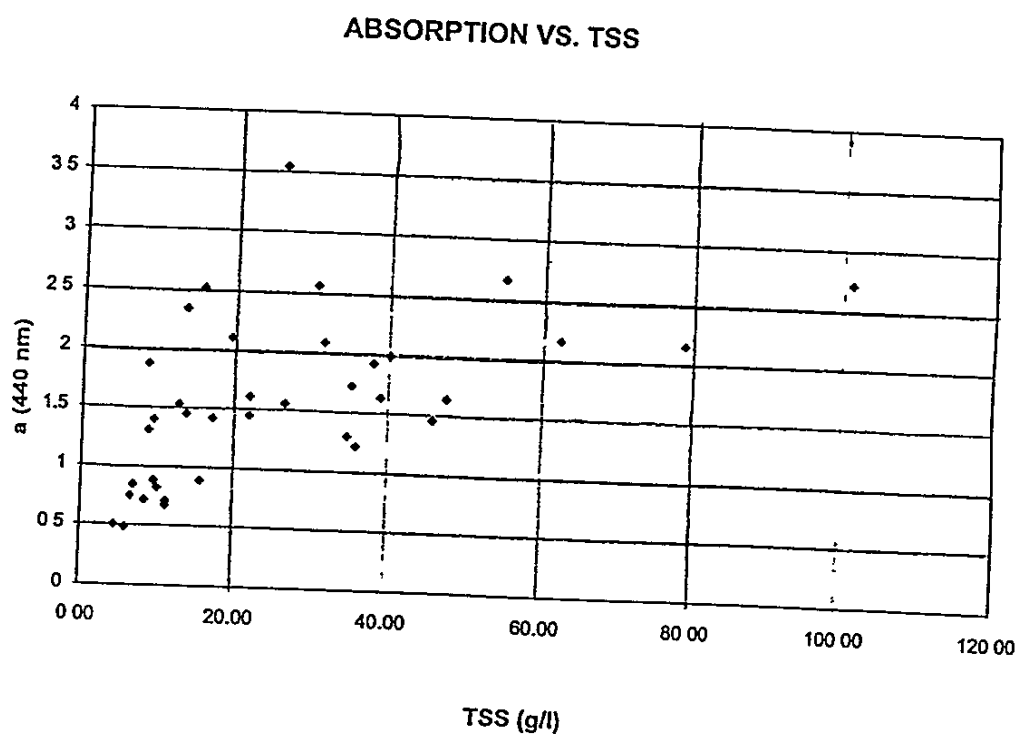


Fig 24 Absorption versus TSS at a wavelength of 440 nm

TOTAL SCATTERING COEFFICIENT VS. TSS

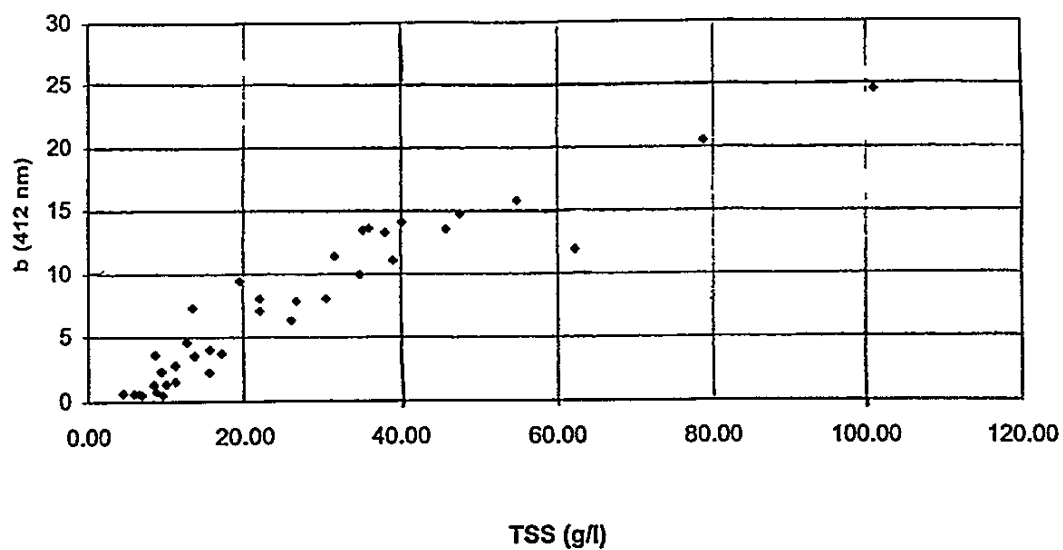


Fig 25. Total scattering coefficient versus TSS at a wavelength of 412 nm.

TOTAL SCATTERING COEFFICIENT VS. TSS

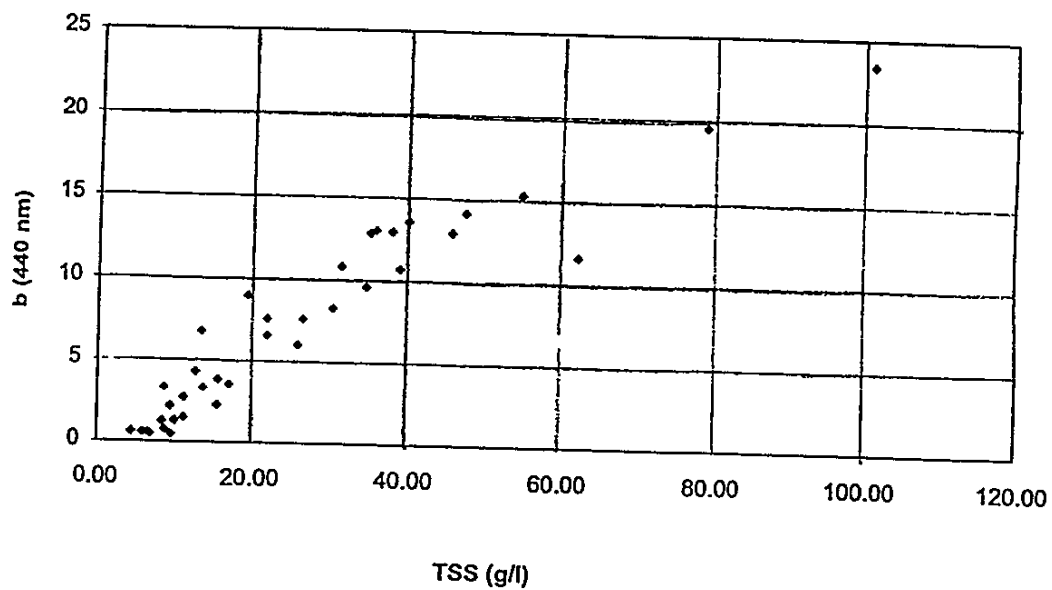


Fig 26. Total scattering coefficient versus TSS at a wavelength of 440 nm.

contain the effect of absorption, so the correlation of b with TSS is expected to be better than it is with c , which is indeed the case with our data set. Thus, except for probably a single outlier at about TSS = 61 g/l, the entire Laguna Madre data set gives an excellent linear correlation of b with TSS. This groundbreaking result should allow us to accurately model the effects of light attenuation due to scattering by suspended sediments in Laguna Madre.

It is of interest to calculate the slope of the IOP's versus TSS for various wavelengths, to investigate what are the wavelength dependence of the slopes. This is important for the overall modeling of PAR as a function of suspended sediment concentrations. Figures 27, 28, and 29 show these results for c , a , and $b = c - a$, respectively. Interestingly, the slope versus wavelength for c is nearly linear. For a , the slope dependence on wavelength is not as simple, but it is still surprisingly monotonic, although it should be remembered that the correlation of a with TSS was not very good. As should be expected, we obtain the "smoothest" relationship of slope versus wavelength the b . In conclusion, we expect to be able to model light attenuation given TSS concentration in Laguna Madre very accurately.

Hydrolight

Exact computations of $E_d(z)$ can be made with the radiative transfer numerical model called Hydrolight. This model requires, as input, the solar insolation, the IOP's of the water column, and, where appropriate, the bottom reflectance. Hydrolight then computes the in-water light-field, from which quantities such as irradiance and PAR can be obtained. Our measurements at Laguna Madre included both the inputs required for Hydrolight and the output computations it produces. Thus, by using Hydrolight, we can verify, in the sense of closure, the consistency of our data sets. Although this is more an academic exercise, it will provide a verification of our results.

SLOPE VS. WAVELENGTH FOR BEAM ATTENUATION COEFFICIENT

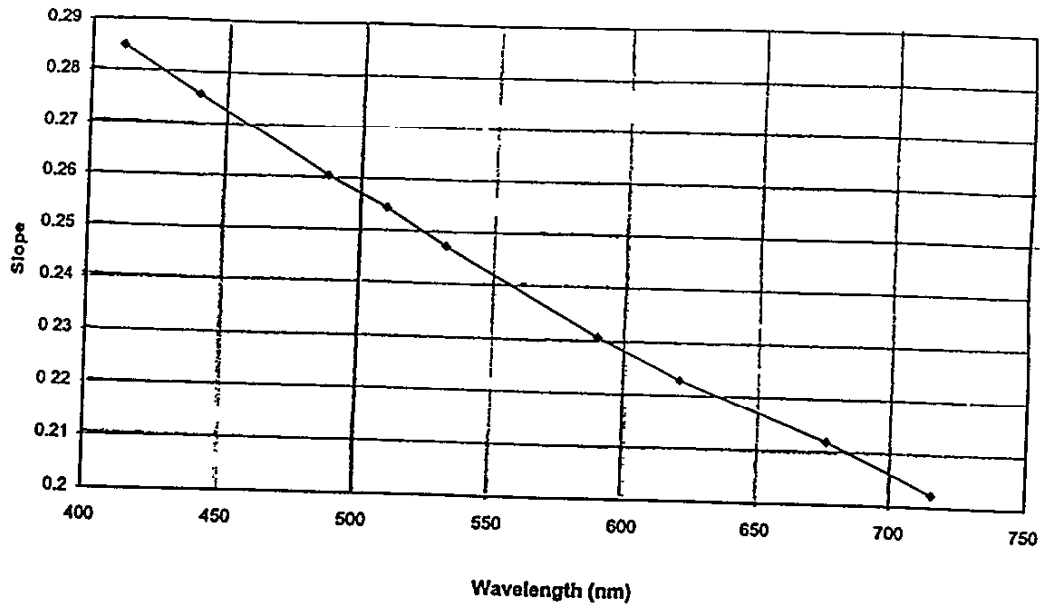


Fig 27. Slope versus wavelength for the beam attenuation coefficient.

SLOPE VS. WAVELENGTH FOR ABSORPTION

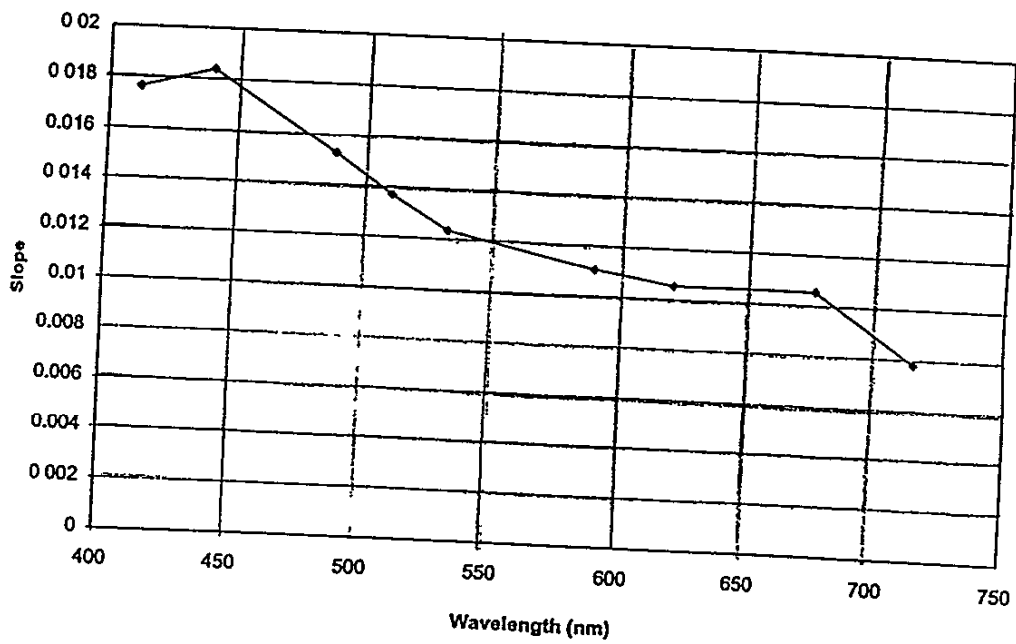


Fig 28. Slope versus wavelength for absorption.

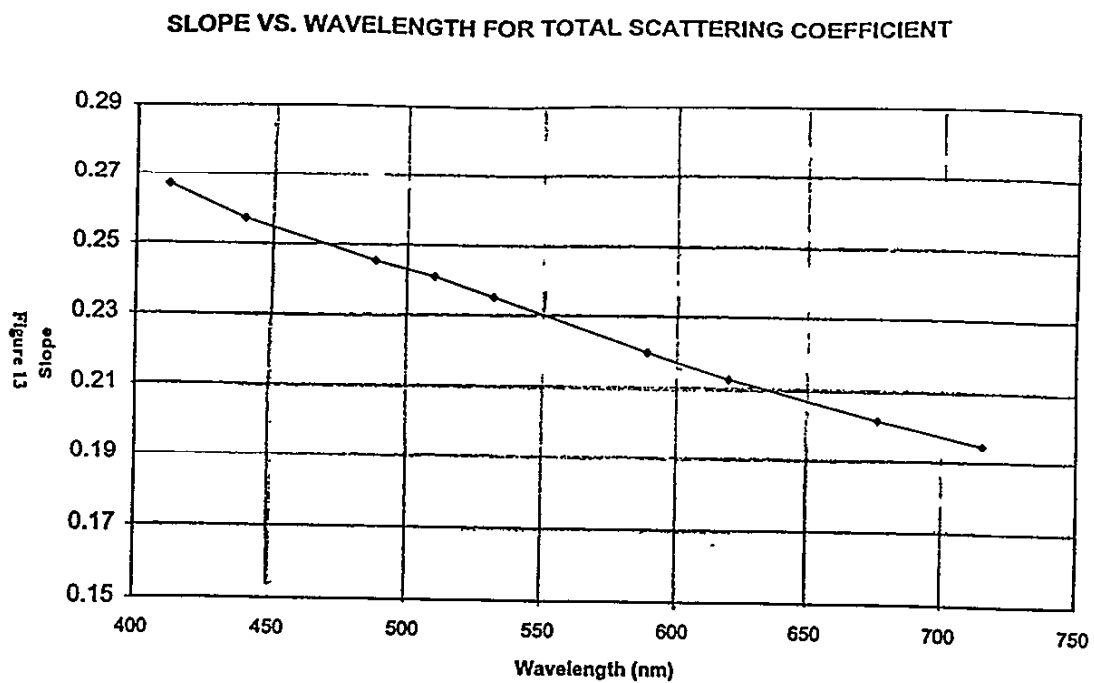


Fig 29. Slope versus wavelength for the scattering coefficient.

Table 6. TSS data taken in conjunction with IOP data in upper and lower Laguna Madre, TX in August 1997.

Date	Sample I.D.	SPM (mg/L)
8/12/97	AC 9.1129-1 LM3	4.54
8/12/97	AC 9.1227-1 LM3	5.95
8/12/97	AC9.1400-1 LM4 26.07.661 N 97.13.345 W	11.25
8/12/97	AC9.1436-1 LM5 100m N Buoy 121	30 43
8/12/97	AC9.1520-1 LM6	38.00
8/12/97	AC9.1642-1 LM7	25.88
8/12/97	AC9.1750-1 LM8	6.95
8/12/97	AC9.1815-1 LM8	15 57
8/13/97	AC 9.1116-1 LM9 26.09.672 N 97.17.363W	8.50
8/13/97	AC 9.1143-1 LM10 26.09.760 N 97.17.083 W	11.25
8/13/97	AC 9.1200-1 LM11 26.09.818 N 97.16.808 W	15.63
8/13/97	AC 9 1228-1 LM12 26.09.918 N 97.16.515 W	35.90
8/13/97	AC 9.1250-1 LM13 26.09.947 N 97.16 177 W	35.18
8/13/97	AC 9.1318-1 LM14 26.10 100 N 97.15.765 W	45.75
8/13/97	AC 9 1340-1 LM15 26 10.100 N 97.15.785 W	34.75
8/13/97	AC 9.1404-1 LM16 26.10.218 N 97.14.962 W	47.5
8/13/97	AC 9.1425-1 LM17 26 10 090 N 97.14.730 W	39.00
8/13/97	AC 9.1444-1 LM18 26 10.378 N 97.14.337 W	40 13
8/13/97	AC 9 1510-1 LM19 26 10.598 N 97 13.761W	26.53
8/13/97	AC 9.1550-1 LM20 26.10 796 N 97.13.253 W	10 10
8/13/97	AC 9.1614-1 LM21 26 10.797 N 97.12.555 W	6.60
8/13/97	AC 9.1631-1 LM22 26.10.899 N 97.11.959 W	9.65
8/13/97	AC 9.1647-1 LM23 26.11.059 N 97.11 429 W	17.08
8/14/97	AC 9.1140-1 LM24 26 37.666 N 97.23.099 W	8.85
8/14/97	AC 9.1230.-1 LM25 26.37.612 N 97.23 417 W	21.88
8/14/97	AC9.1300-1 LM26 26.37.480 N 97.23.701 W	78.75
8/14/97	AC 9.1400-1 LM27 26.37.589 N 97.24.946 W	101.08
8/14/97	AC 9.1426-1 LM28 26.37.533 N 97.29.969 W	62 25
8/14/97	AC 9.1445-1 LM 29 26.37.704 N 97.26 350 W	54.80
8/15/97	AC 9.0940-1 LM30 27.22.038 N 97.21.881 W	21.88
8/15/97	AC 9.1040-1 LM31 27.22 096 N 97.22.428 W	31.50
8/15/97	AC 9 1059-1 LM32 27.22.219 N 97.22.729	19.33
8/15/97	AC 9.1118-1 LM33 27.22.346 N 97.22.956 W	13.43
8/15/97	AC 9.1226-1 LM34 27.28.449 N 97.19.038 W	8.67
8/15/97	AC 9.1256-1 LM35 27.28.380 N 97.19.303 W	9.50
8/15/97	AC 9.1318-1 LM36 27.28.388 N 97.19 529 W	13.70
8/15/97	AC 9.1336-1 LM37 27 28.422 N 97.19.562 W	12.70

Part III: Preliminary Spectral Irradiance Model

Abundant seagrasses are a sign of healthy and productive coastal environments that support a biodiverse fauna. Unfortunately, seagrass densities have been declining in U.S. waters. Consequently, significant state and national resources are being devoted to the study and modeling of seagrasses. Our recent efforts strongly suggest that accepted modeling strategies are not appropriate for predicting the outcome of anthropogenic disturbances. Equivalent light absorption by either sediments or algae will affect seagrass growth differently because of their contrasting light absorbance properties. Although seagrasses have successfully evolved to take advantage of the light/nutrient environment found in Laguna Madre, man-made changes imposed by dredging, and the advent of "brown tide" blooms in the late 1980s have resulted in a significant alteration in the quantity and quality of light.

The seagrass modeling effort is only intended to determine the impacts due to changes in sediment concentration in the water column. Thus, it is important that the model discriminate between impacts due to increasing sediment concentration and those due to other factors (e.g. "brown tide"). As shown in the preliminary modeling described below, models that account for the quality of light (spectral irradiance models), which is impacted differently by sediment and living material, will predict different growth rates compared to established PAR models. However, PAR models are extremely useful because they can employ the available data (PAR, attenuation coefficients, photosynthesis versus irradiance (P vs I) curves). A description of the PAR models used in the seagrass model under development can be found in Chapter 1. We have initiated testing of a spectral irradiance model, which will eventually be added as a module to the present seagrass model. This should allow us to make better predictions of the growth potential of seagrasses under predicted light fields and to assess the relative impact of sediment and living material on seagrass health.

Model Description

The seagrass model will ultimately have components for nutrient limitation and other sediment derived inhibition factors, but these matters will not be addressed in this chapter. Primary production of phytoplankton, drift algae, and seagrass can be calculated from available irradiance, which is measured by the spectral radiometer (EQ 5):

$$P(z) = f(z) 12000 PHAR, \quad (EQ 5)$$

where $P(z)$ is the daily production rate ($\text{mg-C m}^{-3} \text{ d}^{-1}$) at depth z , $PHAR$ is photosynthetically absorbed radiation ($\text{Einstein m}^{-3} \text{ d}^{-1}$), 12,000 is a conversion factor and $f(z)$ is the in situ quantum

yield (Einstein mg Chla a⁻¹ d⁻¹). PHAR is calculated by quantifying photosynthetic absorption spectra of the plant based on the spectral quanta available (EQ 6)

$$PHAR = \int_{400}^{700} Q(z, \lambda) a(\lambda) Chla(z) d\lambda, \quad (EQ 6)$$

where $Q(z, \lambda)$ is spectral quanta (Einstein s⁻¹ m⁻² nm⁻¹), $a(\lambda)$ are absorption coefficients (e.g. “brown tide”, seagrass, drift algae (m² mg⁻¹)) and $Chla(z)$ (mg m⁻³) is a proxy for biomass. In turn, $\phi(z)$ is a function of irradiance and cell physiology and can best be characterized by a variant of the Kiefer-Mitchell model (Bidigare et al. 1987). This formulation defines ϕ_m as the maximum quantum yield, and relates this quantity to $\phi(z)$ using a Monod-like negative feedback. For this purpose K_r' is the P_m scaled by f_m (Einstein mg chla⁻¹ d⁻¹) (EQ 3):

$$\phi(z) = \phi_m \frac{\left(k_{\phi}' Chla(z) \right)}{\left(k_{\phi}' Chla + PHAR(z) \right)}. \quad (EQ 7)$$

Influence of Light Quality on Production

To demonstrate the importance of light quality, we present a conceptual modeling exercise. Five concentrations of a chrysophyte (similar to Brown Tide alga) and of sediment were chosen, such that the resulting absorption coefficients, a_c and a_s , respectively, were similar (Table 1). In turn, available light (PAR and spectral) was calculated as a function of depth (0 to 2 m) similar to those in the Laguna Madre. Although PAR versus depth was equivalent for each case (not shown), regardless of the source of turbidity, the quality of light differed (e.g., Fig. 30). Nutrients were assumed to be non-limiting. To simplify this example, we used the same spectral irradiance model for the chrysophyte and the seagrass (i.e., chlorophyll *a* was the most prevalent pigment in both).

The PAR-based productivity model (Jassby and Platt, 1976) predicted higher production compared to the spectral irradiance model, particularly at high concentrations of chrysophyte or sediment (Table 6). This difference was more evident at depths where seagrasses would grow (see Fig. 31). Also, the disparity between models was significantly greater when the chrysophyte was the source of turbidity because it absorbs light at wavelengths required by plants growing at depth. Finally, scattering was not considered, but this phenomenon should have accentuated this difference (G. Jackson pers. comm.) and will be included in the model described below. Although simplistic,

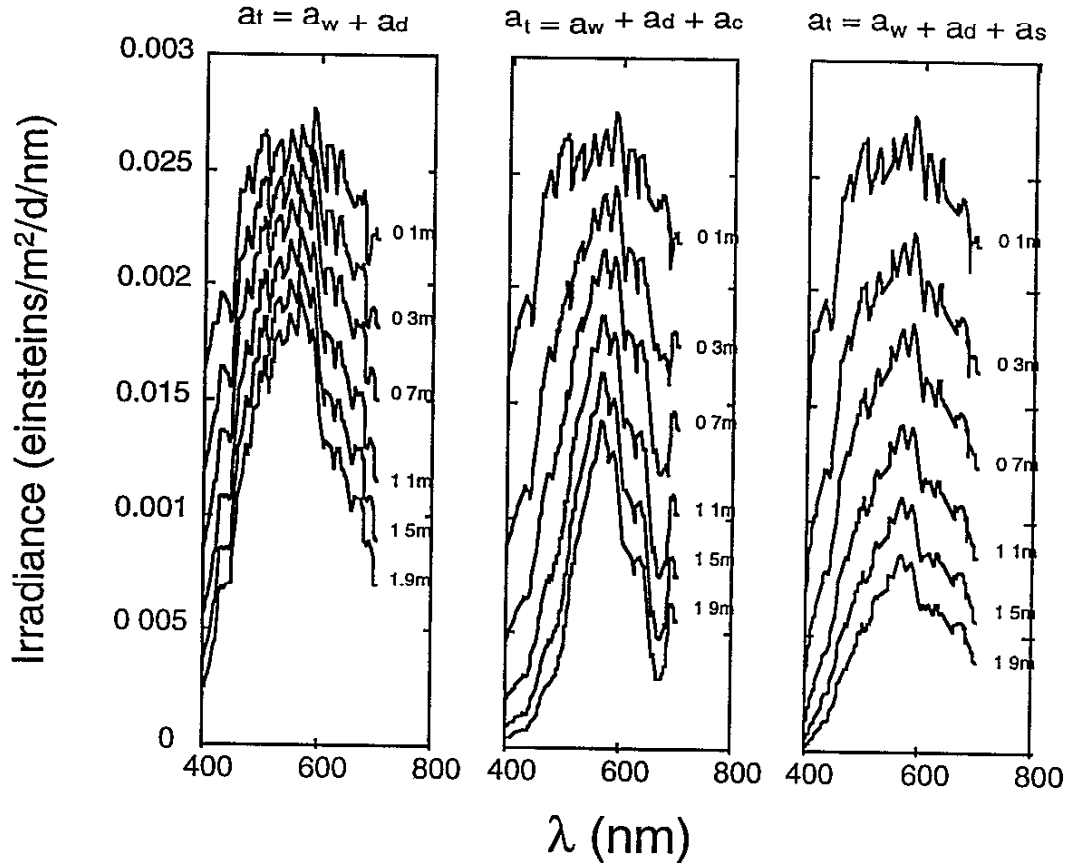


Figure 30. Our simplified radiance transfer model (downwelling light only) predicts spectral irradiance ($\mu\text{mols/m}^2/\text{d}/\text{nm}$) as a function of depth for (left to right) filtered Laguna Madre water, Laguna Madre water with added chrysophyte ($30 \mu\text{g chl } a/l$) and Laguna Madre water with added sediment (50 mg/l). The coefficients, a_w , a_d , a_c , a_s and a_t , are for water, DOM, phytoplankton, sediment and total absorption, respectively. In the latter two cases, a_t are equivalent, which means PAR is also equal at all depths. However, as is evident from the shapes of the curves, spectral quality is quite different, particularly at 650 to 700 nm.

this modeling exercise demonstrates the potential importance of distinguishing the source of light absorption, particularly when comparing the impact of sediment resuspension to that of algal blooms or floating algal mats.

Table 7. Cases used in the comparison of the spectral irradiance model (P_{SPECTRAL}) with the standard PAR model (P_{PAR}). $P_{\text{SPECTRAL}}/P_{\text{PAR}}$ is the ratio of water column integrated production. Also, a_c and a_s are phytoplankton and sediment absorption coefficients, respectively.

Case	[Chlor a] $\mu\text{g/l}$	[SPM] mg/l	a_c	a_s	Phytoplankton $P_{\text{SPECTRAL}}/P_{\text{PAR}}$	Sediment $P_{\text{SPECTRAL}}/P_{\text{PAR}}$
1	0	0	.00	.00	0.99	0.99
2	5	10	.10	.12	0.98	0.98
3	30	50	.61	.60	0.91	0.95
4	60	100	1.2	1.2	0.85	0.93
5	300	500	6.1	6.0	0.79	0.93

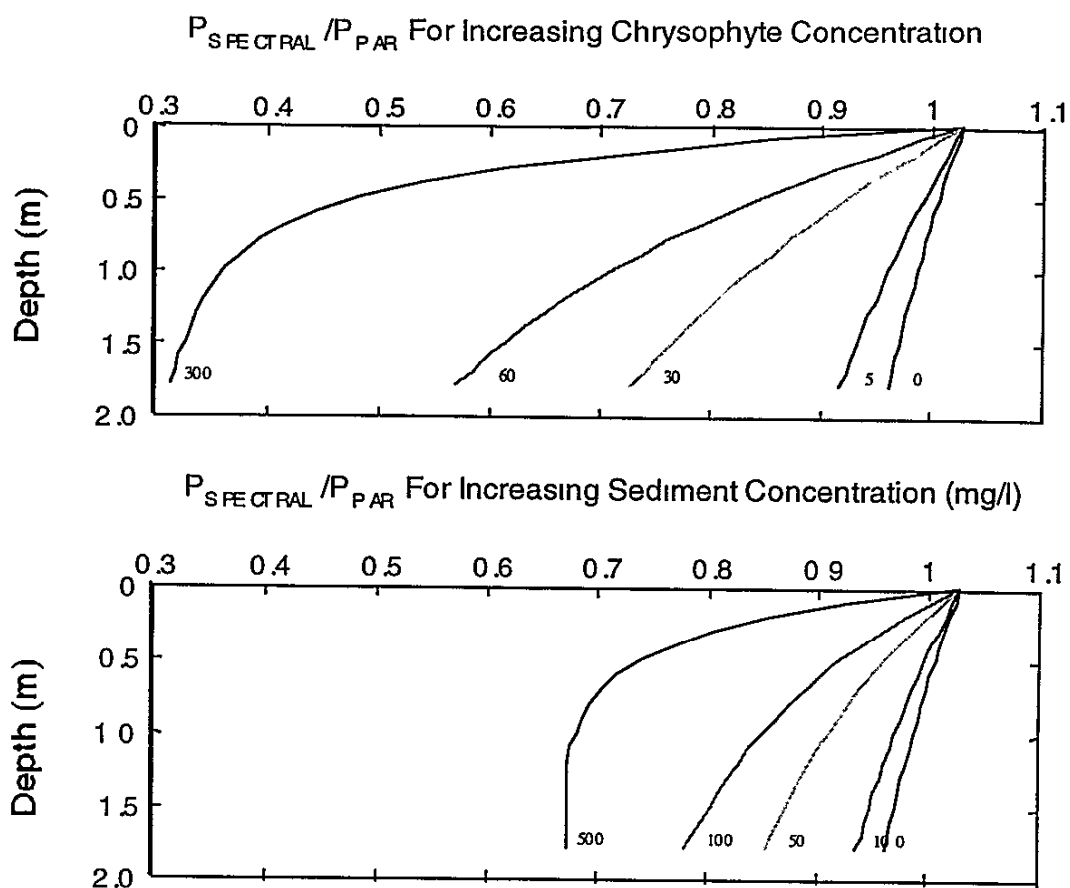


Figure 31. Results of conceptual model showing the ratio of predictions by our spectral irradiance model to predictions by the PAR model (Jassby and Platt, 1976) ($P_{\text{SPECTRAL}} / P_{\text{PAR}}$) as a function of depth (m) for additions of phytoplankton (in $\mu\text{g chl } a/l$) and sediment (mg/l).

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Appendix 1 Pigment data for the fixed sampling stations in Laguna Madre from June 1996 to November 1997. Values represent means and standard deviations B.D = below detection, NS = not sampled and several samples were lost as a result of analytical problems.

Site	date	Chl a	SD	Chl b	SD	Chl c1c2	SD	19 But	SD	19 Hex	SD	Fuco	SD	Prasin	SD	Diadin	SD	Zea	SD
ULM 1	Jun 96	21.0	1.0	3.1	0.2	1.8	0.3	3.9	0.1	B.D	B.D	5.7	0.3	B.D	B.D.	B.D	B.D	1.4	0.5
ULM 2	Jun 96	28.1	1.8	1.1	0.2	10.0	5.3	6.5	0.5	B.D	B.D.	7.6	0.1	0.5	0.7	4.5	1.7	0.9	0.1
ULM 3	Jun 96	43.7	2.2	5.3	0.4	4.0	0.2	8.0	0.3	B.D	B.D	12.7	0.7	B.D.	B.D	B.D.	B.D	2.3	0.2
LLM 1	Jun 96	14.9	0.2	B.D	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.	0.5	0.1	B.D.	B.D	B.D	B.D.	B.D	B.D.
LLM 2	Jun 96	4.5	0.5	B.D	B.D	B.D.	B.D	B.D.	B.D	B.D	B.D.	B.D.	B.D.	B.D	B.D.	1.5	0.4	B.D	B.D.
LLM 3	Jun 96	15.4	1.5	1.9	0.3	1.1	0.9	2.7	0.1	B.D	B.D.	3.9	0.2	0.0	0.0	1.0	0.2	0.9	0.1
ULM 1	Jul 96	7.8	0.8	B.D.	B.D.	0.8	0.1	0.8	0.1	B.D.	B.D.	1.2	0.2	0.1	0.1	B.D	B.D	0.7	0.1
ULM 2	Jul 96	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost
ULM 3	Jul 96	45.7	1.5	B.D	B.D.	4.7	0.2	4.9	0.2	B.D	B.D.	12.9	0.6	1.1	0.2	2.6	0.1	1.1	0.0
LLM 1	Jul 96	5.2	2.3	B.D.	B.D	B.D.	B.D	B.D.	B.D.	B.D	B.D.	1.6	0.8	B.D.	B.D	B.D	B.D.	B.D	B.D.
LLM 2	Jul 96	0.6	0.2	B.D.	B.D.	B.D	B.D.	B.D	B.D.	B.D	B.D.	0.3	0.1	B.D	B.D	B.D	B.D.	0.0	B.D
LLM 3	Jul 96	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
ULM 1	Aug 96	9.2	0.5	B.D.	B.D.	2.4	1.7	1.2	B.D.	B.D	B.D.	B.D.	B.D	B.D.	B.D.	B.D	B.D	0.6	0.1
ULM 2	Aug 96	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost
ULM 3	Aug 96	61.6	7.0	B.D	B.D	0.6	0.1	B.D	B.D	3.6	0.4	18.6	2.5	2.3	0.2	7.2	1.1	B.D	B.D.
LLM 1	Aug 96	2.6	0.3	B.D	B.D	B.D	B.D	B.D	B.D	B.D	B.D.	0.6	0.1	B.D	B.D	B.D	B.D	B.D	B.D
LLM 2	Aug 96	0.8	0.2	B.D	B.D	B.D	B.D.	B.D	B.D	B.D	B.D	B.D	B.D	B.D	B.D	B.D	B.D	B.D	B.D
LLM 3	Aug 96	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
ULM 1	Sept 96	43.3	6.3	B.D	B.D.	2.5	0.2	5.2	1.8	B.D	B.D	9.4	3.7	0.5	0.8	1.7	B.D	0.5	B.D
ULM 2	Sept 96	59.3	13.0	B.D	B.D	5.7	1.0	9.4	0.2	B.D	B.D	2.7	0.2	2.0	B.D	5.8	1.3	0.4	0.1
ULM 3	Sept 96	34.2	6.8	B.D	B.D	3.7	B.D	5.5	B.D	B.D	B.D	11.3	B.D	2.3	B.D	B.D	B.D	0.4	B.D
LLM 1	Sept 96	5.0	0.7	B.D.	B.D	4.4	1.5	0.5	0.1	B.D	B.D.	1.6	0.2	B.D	B.D	0.0	0.0	0.2	0.1
LLM 2	Sept 96	0.6	0.2	B.D	B.D	B.D	B.D	B.D	B.D	B.D	B.D	1.4	1.6	B.D	B.D	B.D	B.D	B.D	B.D
LLM 3	Sept 96	9.9	1.4	B.D.	B.D	2.2	0.3	1.8	0.5	B.D	B.D	2.4	1.1	0.0	0.0	0.7	0.2	0.5	0.5
ULM 1	Oct 96	5.5	0.3	B.D.	B.D.	0.2	0.0	B.D	B.D	B.D	B.D	1.2	0.0	B.D	B.D	0.4	0.0	B.D	B.D
ULM 2	Oct 96	31.5	4.6	B.D	B.D.	0.4	0.0	B.D	B.D	B.D	B.D	7.6	1.1	B.D	B.D	7.6	1.0	B.D	B.D
ULM 3	Oct 96	34.1	4.0	B.D.	B.D.	0.4	0.0	B.D.	B.D.	B.D	B.D	8.3	1.2	B.D	B.D.	7.5	0.9	B.D	B.D
LLM 1	Oct 96	7.9	1.1	B.D	B.D	0.2	0.0	B.D	B.D	B.D.	B.D.	2.0	0.8	B.D	B.D	0.8	0.1	B.D	B.D
LLM 2	Oct 96	0.9	0.1	B.D.	B.D.	B.D.	B.D.	B.D.	B.D	B.D	B.D.	B.D	B.D.	B.D.	B.D.	B.D.	B.D	B.D	B.D.
LLM 3	Oct 96	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
ULM 1	Nov 96	4.8	0.9	B.D.	B.D.	B.D.	B.D.	B.D.	B.D.	B.D	B.D.	1.4	0.3	B.D	B.D	B.D.	B.D.	B.D	B.D
ULM 2	Nov 96	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost
ULM 3	Nov 96	38.1	2.1	B.D.	B.D.	3.3	0.4	B.D	B.D.	B.D	B.D	9.1	1.7	B.D.	B.D.	B.D	B.D	Lost	Lost
LLM 1	Nov 96	2.3	0.3	B.D.	B.D.	B.D	B.D	B.D	B.D.	B.D	B.D	0.6	0.0	B.D.	B.D	B.D	B.D	B.D	B.D
LLM 2	Nov 96	0.7	0.3	B.D.	B.D.	B.D.	B.D	B.D.	B.D	B.D	B.D	B.D.	B.D.	B.D	B.D	B.D.	B.D	B.D	B.D

Site	date	Chl a	SD	Chl b	SD	Chl c1c2	SD	19 But	SD	19 Hex	SD	Fuco	SD	Prasin	SD	Diadin	SD	Zea	SD
LLM 3	Nov 96	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
ULM 1	Dec. 96	74	04	BD	BD	02	00	02	BD	02	01	20	00	B.D.	B.D	B.D.	BD	01	00
ULM 2	Dec. 96	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost	Lost
ULM 3	Dec. 96	66.4	16	BD	BD	07	00	BD	BD	15	03	14.1	1.8	B.D.	B.D.	B.D	BD	03	01
LLM 1	Dec 96	43	15	B.D.	B.D.	BD	B.D.	B.D.	B.D	BD	BD	13	05	BD	BD	BD	B.D.	01	00
LLM 2	Dec 96	21	04	BD	BD	B.D	B.D.	BD	BD	BD	BD.	06	01	B.D.	B.D	B.D.	B.D.	BD	B.D
LLM 3	Dec. 96	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
ULM 1	Jan 97	28	05	BD	B.D.	B.D	BD	BD	B.D	BD	B.D	04	00	BD	BD	BD	B.D.	BD	B.D.
ULM 2	Jan. 97	13.1	22	BD	BD	B.D.	B.D.	BD	BD	BD	BD	09	02	BD	BD	05	01	BD	B.D.
ULM 3	Jan. 97	27.9	29	48	02	02	00	BD	BD	BD	BD	18	01	BD	BD	09	03	BD	BD
LLM 1	Jan 97	32	10	B.D.	B.D.	BD	BD	B.D.	BD	B.D	B.D.	07	03	B.D.	B.D.	B.D.	B.D.	BD	BD
LLM 2	Jan. 97	18	02	B.D.	B.D.	01	00	BD	B.D	B.D.	B.D.	05	01	BD	B.D.	B.D.	BD	BD	BD
LLM 3	Jan 97	40.5	22	5.8	0.4	0.5	00	BD	BD	11	01	79	07	BD	BD	27	05	BD	BD
ULM 1	Feb 97	32	07	B.D.	B.D.	BD	BD	BD	BD	B.D	B.D.	1.1	02	B.D.	B.D.	B.D.	B.D.	BD	BD
ULM 2	Feb. 97	31	03	B.D.	BD	B.D.	B.D.	BD	BD	BD	BD	08	01	BD	BD	B.D	B.D	BD	BD
ULM 3	Feb 97	33.4	2.9	B.D	BD	05	00	B.D.	B.D.	15	03	90	18	BD	BD	BD	BD	02	01
LLM 1	Feb 97	19.8	18	BD	BD	03	00	14	02	BD	BD	58	11	BD	BD	34	05	08	02
LLM 2	Feb. 97	18.3	05	B.D	B.D.	0.3	00	15	02	B.D.	B.D.	50	0.6	B.D.	B.D	34	04	B.D.	B.D
LLM 3	Feb 97	21.3	09	1.5	02	02	00	BD	B.D.	BD	BD	26	02	BD	BD	BD	BD	BD	BD
ULM 1	Mar 97	43	10	B.D.	B.D.	01	00	BD	BD	B.D	B.D.	10	02	BD	BD	02	00	BD	BD
ULM 2	Mar 97	14.2	10	2.8	03	02	01	BD	B.D.	04	01	27	03	B.D.	B.D	06	00	B.D	BD
ULM 3	Mar. 97	28.7	16	B.D.	B.D.	0.3	00	21	00	13	01	77	05	BD	BD	BD	BD	07	01
LLM 1	Mar 97	56.5	05	B.D.	B.D.	0.6	01	BD	BD	12	01	149	02	BD	BD	BD	BD	06	00
LLM 2	Mar. 97	1.2	01	BD	BD	BD	BD	B.D.	B.D	BD	B.D.	0.3	01	B.D.	BD	01	00	B.D.	B.D
LLM 3	Mar. 97	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
ULM 1	Apr 97	63	0.2	B.D	B.D.	02	00	BD	BD	B.D.	BD	13	02	BD	BD	04	00	01	00
ULM 2	Apr 97	21.7	32	2.2	03	02	00	BD	BD	B.D	BD	30	09	1.5	03	1.1	02	BD	BD
ULM 3	Apr 97	28.4	1.1	24	01	03	00	BD	BD	08	03	47	10	B.D	B.D	21	01	02	00
LLM 1	Apr 97	120	1.3	11	01	02	00	09	01	BD	BD	24	02	B.D	BD	13	03	06	01
LLM 2	Apr 97	300	1.5	BD	B.D.	0.5	00	BD	BD	B.D	B.D.	51	0.9	BD	BD	17	01	02	00
LLM 3	Apr 97	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
ULM 1	May 97	6.8	0.1	B.D.	B.D.	BD	BD	B.D	BD	BD	BD	22	01	BD	BD	BD	BD	03	00
ULM 2	May 97	33.6	0.8	BD	B.D.	05	00	BD	BD	14	01	98	03	B.D	B.D.	BD	BD	05	00
ULM 3	May 97	36.7	03	BD	BD	04	00	B.D.	B.D.	12	01	101	05	BD	BD	BD	BD	05	00
LLM 1	May 97	14.9	08	B.D	B.D.	04	00	B.D	BD	BD	BD	25	04	07	01	BD	BD	06	00
LLM 2	May 97	0.2	0.1	B.D.	BD	05	BD	BD	BD	B.D	B.D.	B.D.	B.D.	BD	BD	BD	BD	BD	BD
LLM 3	May. 97	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
ULM 1	Jun 97	79	0.3	1.3	01	BD	B.D.	BD	B.D.	BD	BD.	07	02	BD	BD	BD	BD	06	00
ULM 2	Jun 97	18.3	2.9	0.9	0.1	02	00	B.D	BD	0.8	02	4.3	1.5	BD	BD	20	09	BD	BD

Site	date	Chl a	SD	Chl b	SD	Chl c1c2	SD	19 But	SD	19 Ilcx	SD	Fuco	SD	Prasin	SD	Diadin	SD	Zea	SD
ULM 3	Jun 97	20.8	0.7	1.7	0.1	0.2	0.0	BD	BD	0.4	0.1	3.2	1.1	BD	BD	1.0	0.1	BD	BD
LLM 1	Jun 97	8.1	1.2	1.0	0.2	BD	BD	BD	BD	BD	BD	BD	BD	2.0	0.5	BD	BD	0.3	0.1
LLM 2	Jun 97	0.4	0.2	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD
LLM 3	Jun 97	14.4	1.6	1.6	0.3	0.2	0.0	BD	BD	0.4	0.0	2.5	0.3	BD	BD	0.8	0.1	0.6	0.1
ULM 1	Jul 97	5.6	0.4	BD	BD	BD	BD	BD	BD	BD	BD	1.1	0.1	BD	BD	0.8	0.1	BD	BD
ULM 2	Jul 97	1.2	0.1	BD	BD	BD	BD	BD	BD	BD	BD	0.2	0.0	BD	BD	0.3	0.0	BD	BD
ULM 3	Jul 97	6.8	0.2	BD	BD	0.1	0.0	BD	BD	BD	BD	0.6	0.1	BD	BD	1.7	0.1	BD	BD
LLM 1	Jul 97	3.9	0.4	BD	BD	0.1	0.0	BD	BD	BD	BD	0.9	0.3	BD	BD	0.2	0.0	0.2	0.1
LLM 2	Jul 97	0.1	0.2	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD
LLM 3	Jul 97	4.0	0.6	BD	BD	0.2	0.0	BD	BD	BD	BD	0.6	0.1	0.2	0.0	BD	BD	BD	BD
ULM 1	Aug 97	10.2	0.2	BD	BD	0.2	0.0	2.4	0.6	0.4	0.1	0.5	0.1	BD	BD	1.1	0.0	BD	BD
ULM 2	Aug 97	3.1	0.4	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD	0.2	0.1	BD	BD	0.6	0.1
ULM 3	Aug 97	6.2	0.8	1.0	0.1	BD	BD	BD	BD	BD	BD	0.9	0.0	0.2	0.1	0.5	0.1	0.1	0.0
LLM 1	Aug 97	0.5	0.2	BD	BD	0.3	0.0	BD	BD	BD	BD	3.1	0.7	0.3	0.1	3.2	0.7	BD	BD
LLM 2	Aug 97	4.8	0.2	BD	BD	0.1	0.0	BD	BD	BD	BD	0.5	0.0	BD	BD	0.2	0.0	0.5	0.0
LLM 3	Aug 97	7.0	0.7	BD	BD	BD	BD	BD	BD	BD	BD	1.0	0.1	BD	BD	0.3	0.0	0.7	0.1
ULM 1	Sept 97	6.5	0.5	BD	BD	BD	BD	BD	BD	BD	BD	1.0	0.2	BD	BD	0.3	0.0	0.3	0.0
ULM 2	Sept 97	2.0	0.1	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD	0.2	0.0
ULM 3	Sept 97	4.1	0.1	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD	0.6	0.0
LLM 1	Sept 97	0.5	0.1	BD	BD	BD	BD	BD	BD	BD	BD	0.9	0.1	BD	BD	BD	BD	BD	BD
LLM 2	Sept 97	3.0	0.3	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD	0.2	0.0	BD	BD
LLM 3	Sept 97	4.6	0.4	BD	BD	BD	BD	BD	BD	BD	BD	0.3	0.0	BD	BD	0.2	0.0	0.2	0.0
ULM 1	Oct 97	1.9	0.3	BD	BD	BD	BD	0.5	0.1	BD	BD	BD	BD	BD	BD	BD	BD	BD	BD
ULM 2	Oct 97	6.3	0.4	BD	BD	BD	BD	BD	BD	BD	BD	0.4	0.1	0.3	0.0	BD	BD	BD	BD
ULM 3	Oct 97	6.0	0.9	BD	BD	BD	BD	BD	BD	BD	BD	0.5	0.1	BD	BD	0.3	0.1	BD	BD
LLM 1	Oct 97	4.7	0.6	BD	BD	0.2	0.0	BD	BD	BD	BD	1.0	0.1	0.5	0.1	0.4	0.0	BD	BD
LLM 2	Oct 97	2.0	0.1	BD	BD	BD	BD	BD	BD	BD	BD	0.5	0.0	BD	BD	0.3	0.0	BD	BD
LLM 3	Oct 97	11.1	0.3	BD	BD	0.2	0.0	BD	BD	0.6	0.1	1.5	0.1	BD	BD	1.4	0.1	0.4	0.0
ULM 1	Nov 97	3.7	0.1	BD	BD	BD	BD	BD	BD	BD	BD	0.6	0.0	BD	BD	BD	BD	BD	BD
ULM 2	Nov 97	4.5	0.6	BD	BD	BD	BD	BD	BD	BD	BD	0.9	0.1	BD	BD	0.4	0.0	0.6	0.1
ULM 3	Nov 97	7.0	0.5	BD	BD	BD	BD	BD	BD	BD	BD	1.4	0.1	BD	BD	BD	BD	BD	BD
LLM 1	Nov 97	5.0	0.5	BD	BD	BD	BD	BD	BD	BD	BD	1.2	0.2	BD	BD	0.3	0.0	BD	BD
LLM 2	Nov 97	3.8	0.3	BD	BD	BD	BD	BD	BD	BD	BD	0.4	0.0	BD	BD	0.3	0.0	1.0	0.1
LLM 3	Nov 97	0.7	0.0	BD	BD	BD	BD	BD	BD	BD	BD	0.2	0.0	BD	BD	BD	BD	BD	BD

Chapter V: Characterization of Seagrasses, Light, and Water Column Parameters

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CHAPTER V: CHARACTERIZATION OF SEAGRASSES, LIGHT, AND WATER COLUMN PARAMETERS

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Abstract

Continuous measurements of photosynthetically active radiation (PAR), seagrass abundance, and water column chemical parameters were measured at several stations in Laguna Madre over an 18-month period starting in April 1996. PAR showed clear seasonal trends; lowest values were recorded in winter and highest in summer (15 and $60 \text{ mol m}^{-2} \text{ d}^{-1}$ respectively). Average water transparency was clearly highest of station LLM 2 ($k = 0.7 \text{ m}^{-1}$) which was surrounded by dense seagrass beds, and lowest at LLM 1 ($k = 2.4 \text{ m}^{-1}$), an unvegetated site. The decline in the brown tide algal bloom in the upper Laguna led to significant increases in water clarity, at ULM 3, k values over 7.0 m^{-1} in January 1997 declined to less than 2 m^{-1} by June. Water column chlorophyll levels were generally $<10 \text{ } \mu\text{g L}^{-1}$ in the lower Laguna, and declined in the upper Laguna from $20\text{--}70 \text{ } \mu\text{g L}^{-1}$ to $<10 \text{ } \mu\text{g L}^{-1}$ following the decline in the brown tide algal bloom. Nitrate and ammonium levels were generally less than $3 \text{ } \mu\text{M}$ and salinity ranged from $30\text{--}45 \text{ } \text{‰}$ at all sites.

The density and above- and below- ground biomass of the three predominant seagrass species (*Halodule wrightii*, *Thalassia testudinum* and *Syringodium filiforme*) showed distinct seasonal changes that reflected changes in both daylength and water temperature. Ratios of below-ground to above-ground biomass were highest in winter (3-8) and lowest in summer (2-6). *Thalassia* exhibited the highest biomass (over 900 gdw m^{-2}), but highest shoot density was characteristic of *Halodule* (over $8,000 \text{ m}^{-2}$), with *Syringodium* intermediate between the two species. Carbon content in *Thalassia* leaf and rhizome tissues averaged 36%; the nitrogen content of leaf tissues (1.7-2.7%) was higher than that of rhizomes ($<1\%$). Both nitrogen and carbon content exhibited distinct variations as a function of leaf age.

Introduction

The distribution and primary productivity of submerged aquatic vegetation is largely regulated by variations in light attenuation within the water column. In coastal regions, declines in water quality from human encroachment have caused worldwide losses in the distribution of seagrasses (reviewed by Dennison *et al* 1993). In Texas, the documented loss of over 140 km² of seagrasses in the lower Laguna Madre since the 1960's is attributed to decreased water transparency from maintenance dredging (Quammen and Onuf 1993, Onuf 1994); the nearly complete loss of seagrass beds in Galveston Bay (over 20 km²) is also attributed to decreased water transparency and eutrophic conditions that resulted from wastewater discharges, subsidence and dredging activities (Pulich and White 1991).

Light energy has long been recognized as the most important factor influencing seagrass habitats (Zieman and Wetzel 1980), but there are few long-term measurements of *in situ* irradiance. In addition, although the photosynthetic characteristics of several seagrasses have been determined (Drew 1979, Libes 1986, Marsh *et al* 1986, Fouquerean and Zieman 1991, Perez and Romero 1992), this photosynthetic data has not been applied to *in situ* measurements of irradiance. The long term *in situ* measurements irradiance, plant photosynthesis, and seagrass biomass in the Laguna Madre represent a notable exception (Dunton 1994, Dunton and Tomasko 1994). The presence of these data, along with measurements of incident irradiance, growth and biomass, present a rare opportunity for modeling seagrass production and biomass with respect to changes in the underwater light field.

Changes in the amount of light that reaches the bottom are primarily regulated by concentrations of total suspended solids (TSS) and chlorophyll (chl), which can vary widely. The contribution made by TSS and chl largely determine the magnitude of the diffuse light attenuation coefficient (*k*). The relative importance of both can vary across broad spatial and temporal scales. In San Antonio Bay, the resuspension of solids contribute most to light attenuation (Dunton 1996). In other systems, high chlorophyll concentrations result from increased levels of dissolved

inorganic nitrogen that are often derived from anthropogenic inputs (sewage or fertilizers). In either case, light limitation can be assessed from increases in leaf chl content in some seagrass species (e.g., *Thalassia*) that attempt to photoacclimate to maintain high photosynthetic activity.

This chapter presents the 18-mo compilation of *in situ* measurements collected in the Laguna Madre on underwater and surface irradiance, plant biomass and density, various water column parameters (e.g., chl & nutrients), and seagrass blade constituents. The data set focuses on the three species of seagrasses prevalent in the Laguna Madre: *Halodule wrightii* in the upper Laguna and in the lower Laguna, *Thalassia testudinum* and *Syringodium filiforme*. Much of the information presented here was used in the development of an integrative productivity model for all three species.

Methods

Photon flux measurement

Photosynthetically active radiation (PAR 400-700 nm) was collected continuously at six permanent stations (Table 1). At each site a LI-193SA spherical quantum sensor was deployed at canopy level with a LI-1000 datalogger (LI-COR Inc.). The datalogger was placed in a weighted clear polycarbonate housing (Ikelite Model 5910, Indianapolis, IN) and was wired to the sensor cables through molded underwater connectors (Crouse-Hinds Series 41 Penetrator, LaGrange, NC). Sensors were mounted on a 3-cm diameter PVC pipe at canopy level (usually 15-20 cm above the bottom) to minimize fouling by drift algae and seagrass leaves. At all sites, a clear polyethylene bag was placed over the sensor to minimize biofouling of the sensor globe and was replaced at 10-14 day periods to minimize fouling. The polyethylene bag has a negligible effect on light measurements. Photon flux density (PFD: $\mu\text{mol m}^{-2} \text{s}^{-1}$) was measured at 1-min intervals and integrated hourly. Daily PFD ($\text{mol m}^{-2} \text{d}^{-1}$) was calculated as the summation of quantum flux over each 24 hr period.

Coincident measurements of surface PFD was also collected at three stations (ULM-1, ULM-3, and LLM-2) using a LI-190SA quantum sensor and datalogger. This data was used in calculating percent surface irradiance (%SI) and values for the diffuse attenuation coefficient, k . Measurements of depth are average depths, based on numerous soundings that were collected at the study sites by field technicians. Since total tidal amplitudes generally range less than 20 cm, are significantly influenced by prevailing winds, and tide gauge information is not available throughout the Laguna, correction of k for slight changes in depth were not made. Light attenuation was calculated using the Beer-Lambert equation:

$$I_0 = I_z e^{-kz}$$

where I_0 is irradiance at the surface, I_z is irradiance at depth z and k is the attenuation coefficient (m^{-1}). The sensors used in this study were calibrated to $\pm 5\%$ (traceable to National Bureau of Standards), stability was $\pm 2\%$ over any 1 yr period, and data was recorded with a precision of $\pm 0.01 \mu mol m^{-2} s^{-1}$.

Table 1. Permanent sampling stations.

Station	Established	Latitude	Longitude	Physical Description	Biological	Depth (m)
ULM 1	6/17/96	27°41'30"	97°13'20"	ICWW	Bare	1.0
ULM 2	4/1/96*	27°25'02.3"	97°21.288'	100 m East of ICWW	<i>Halodule</i>	1.0
ULM 3	6/17/96	27°11'33"	97°25'42"	ICWW	Bare	1.0
LLM 1	6/4/96	26°11'	97°13'	West of ICWW	Bare	1.15
LLM 2	6/4/96	26°08'	97°12'	1.0 km East of ICWW	<i>Thalassia</i>	1.20
LLM 3	3/1/97	26°35'25.3"	97°22'56.9"	6.0 km East of Port Mansfield	<i>Syringodium</i>	1.27

*Platform not installed at this station

Seagrass density and biomass measurements

Indices of seagrass abundance (density and biomass) were measured in June 1996 at 12 stations (four stations per species) on a transect that extended the entire length of the Laguna (Fig. 1). Depths at the twelve stations ranged from 0.7 m (*Syringodium*) to 1.65 m (*Thalassia*), but were generally in the 0.8-1.1 m range (Table 2). In addition, standing stock was assessed at three stations (each representing one of the predominant species) over a 12-month period at 3-4 month intervals. On each occasion, four replicate samples were collected with a 9 cm diameter coring device for *Halodule* and *Syringodium*, while a 15 cm diameter core was used for *Thalassia*. Samples were thoroughly cleaned of epiphytes and sediments, separated into above-ground and below-ground live biomass and dried at 60°C to a constant weight. Shoot density was estimated by counting the number of shoots per core and scaling to appropriate units (shoots m⁻²).

Water column parameters

Water column physicochemical measurements were collected on two transects that extended the entire length of the Laguna on 3 June 1996 and again on 27 January 1997. Continuous measurements of chlorophyll *a* in the water column were determined using a Morgan 10-AU fluorometer equipped with a continuous flow 25 mm cuvette. In addition, monthly sampling was conducted at the six permanent stations (Table 1) over the entire period of this study. Total DIN ($\text{NO}_3^- + \text{NO}_2^- + \text{NH}_4^+$) and chlorophyll *a* were determined from four replicate water samples collected at each site. Chlorophyll *a* samples were filtered onto cellulose nitrate filters, and then extracted with 90% acetone buffered with 0.05% MgCO_3 and analyzed on a spectrophotometer at 750, 664, 647 and 630 nm following Parsons *et al* (1984). DIN was determined colorimetrically according to Parsons *et al* (1984). Temperature was measured *in situ* using a stem thermometer; salinity was measured using an Orion Model 140 conductivity-salinity meter.

Figure 1 Map of the Laguna Madre showing the location of permanent sampling stations (ULM 1-3; LLM 1-3) and transect stations. Each COE transect site has a corresponding station # which is listed in Table 2.

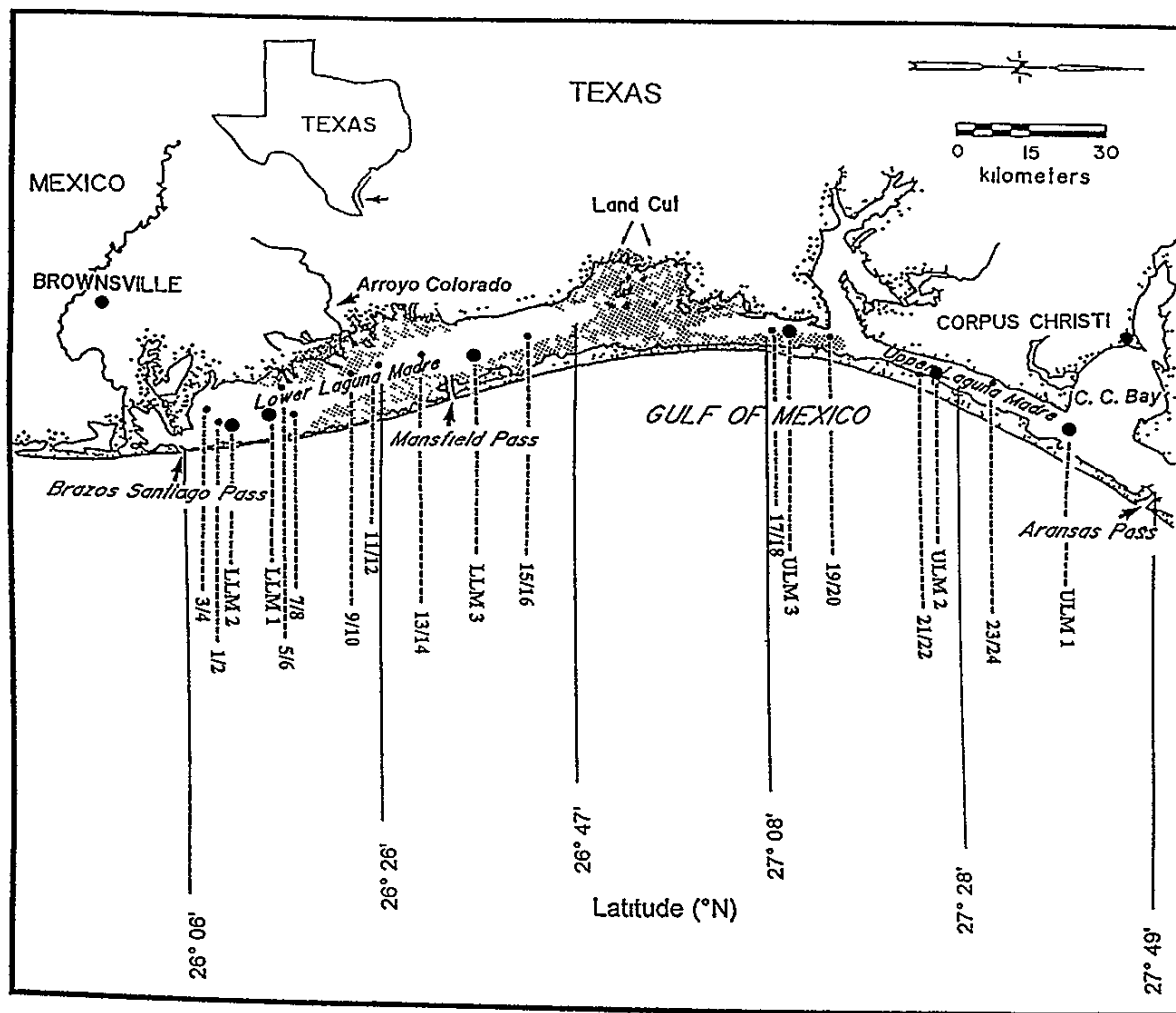


Table 2 Sampling stations along the Laguna Madre transect

COE #	Station	Marker	Latitude	Longitude	Physical Description	Biological	Depth (m)
1 / 2	30 S/B	123	26°08'05 8"	97°12'30 9"	1 0 km East of ICWW	<i>Thalassia</i>	1 2
3 / 4	29 S/B	115	26°07'57 5"	97°14'20 7"	1 0 km West of ICWW	Deep <i>Thalassia</i>	1 65
5 / 6	28 S/B	91	26°11'	97°17'	East of ICWW	<i>Thalassia</i>	1 3
7 / 8	27 S/B	91	26°11'	97°13'	West of ICWW	<i>Thalassia</i>	1 15
9/10	26 S/B	9	26°20'30"	97°21'	East of ICWW - on spoil bank near mouth of Arroyo Colorado	<i>Syringodium</i>	0 9
11/12	25 S/B	7	26°21'	97°19'	West of ICWW - natural bed near Arroyo Colorado	<i>Syringodium</i>	0.7
13/14	24 S/B	159	26°30'23.4"	97°22'44 3"	2 0 km East of ICWW	<i>Syringodium</i>	0 8
15/16	22 S/B	103	26°40'	97°24'	3 0 km East of ICWW	<i>Syringodium</i>	0 8
17/18	20 S/B	47	27°10'47 5"	97°25'45 5"	Old Blucher Remote	<i>Halodule</i>	1 1
19/20	18 S/B	3	27°16'20"	97°24'	East of ICWW	<i>Halodule</i>	1 1
21/22	16 S/B	151	27°25'	97°21'	100 m East of ICWW	<i>Halodule</i>	1 2
23/24	13 S/B	114	27°15'	97°20'45"	King Ranch	<i>Halodule</i>	1 2

S/B : Paired-site combination of seagrass and bare habitats

Blade constituent analysis

Blade chlorophyll (chl) content was determined for six replicate samples from each sampling date. Pre-weighed leaf tissue was ground in 90% cold acetone buffered with 0.05% MgCO_3 using chilled pestles and mortars with washed sea sand. Extracts were made up to a known volume and centrifuged. Absorbance was measured at 750, 664, and 647 nm with a Shimadzu UV 160U spectrophotometer. Chlorophyll *a* and *b* contents were determined using the equations of Jeffrey and Humphrey (1975) for 90% acetone extractions. Subsamples of dried plant

material were taken from biomass cores and used to determine total carbon and nitrogen content. Samples of 1-2 mg were weighed into tin boats for elemental analysis using a Carlo Erba EA 1108 elemental analyzer.

Results

Water column characteristics

On both June and January transects, the presence of the brown tide algal bloom was reflected in high (40-80 $\mu\text{g chl L}^{-1}$) pigment levels. The bloom was densest in the upper Laguna in June (Fig 2), and the Land Cut area to the south in January 1997 (Fig. 3) The shift appears to be a consequence of predominant northerly winds which pushed the bloom southward in winter. Light attenuation was greatest in areas having the highest chlorophyll levels, and lowest nearest the passes. Nitrate and ammonium levels were generally less than 3 μM and salinity ranged from 30 to 45 ppt

Water column chl concentrations from the permanent upper Laguna Madre stations (ULM 1, 2 and 3) were much higher than those of lower Laguna Madre stations (LLM 1, 2 and 3) (Fig. 4). Chlorophyll levels at ULM sites 2 and 3 exhibited their highest levels during summer and fall, but dropped precipitously by June 1997, when the seven-year brown tide bloom in Laguna Madre ended. Water column chl concentrations at ULM 1 in Corpus Christi Bay were considerably lower than at sites ULM 2 and 3 throughout the study period. In the lower Laguna Madre, the pattern was the opposite; water column chl levels reached a peak in late winter (March and April) and were lowest during the summer months. In summer, the average chl concentration in upper Laguna Madre (*ca* 30 $\mu\text{g chl L}^{-1}$) was approximately three times that of lower Laguna Madre (*ca* 10 $\mu\text{g chl L}^{-1}$). Except for the brief winter peak, chlorophyll concentrations in the lower Laguna were generally less than 10 $\mu\text{g chl L}^{-1}$ compared to 20-70 $\mu\text{g chl L}^{-1}$ in the upper Laguna. Ammonium (Fig. 5) and nitrate + nitrite (Fig 6) concentrations were generally low (<3.0 μM) at all stations throughout the entire study period, with the exception of a fall peak (5-8 μM) at the ULM 1 site in October 1997.

Figure 2. Variations in water column chlorophyll *a* with respect to other water column parameters measured along a transect from Corpus Christi Bay to Port Isabel, Texas on June 3, 1996

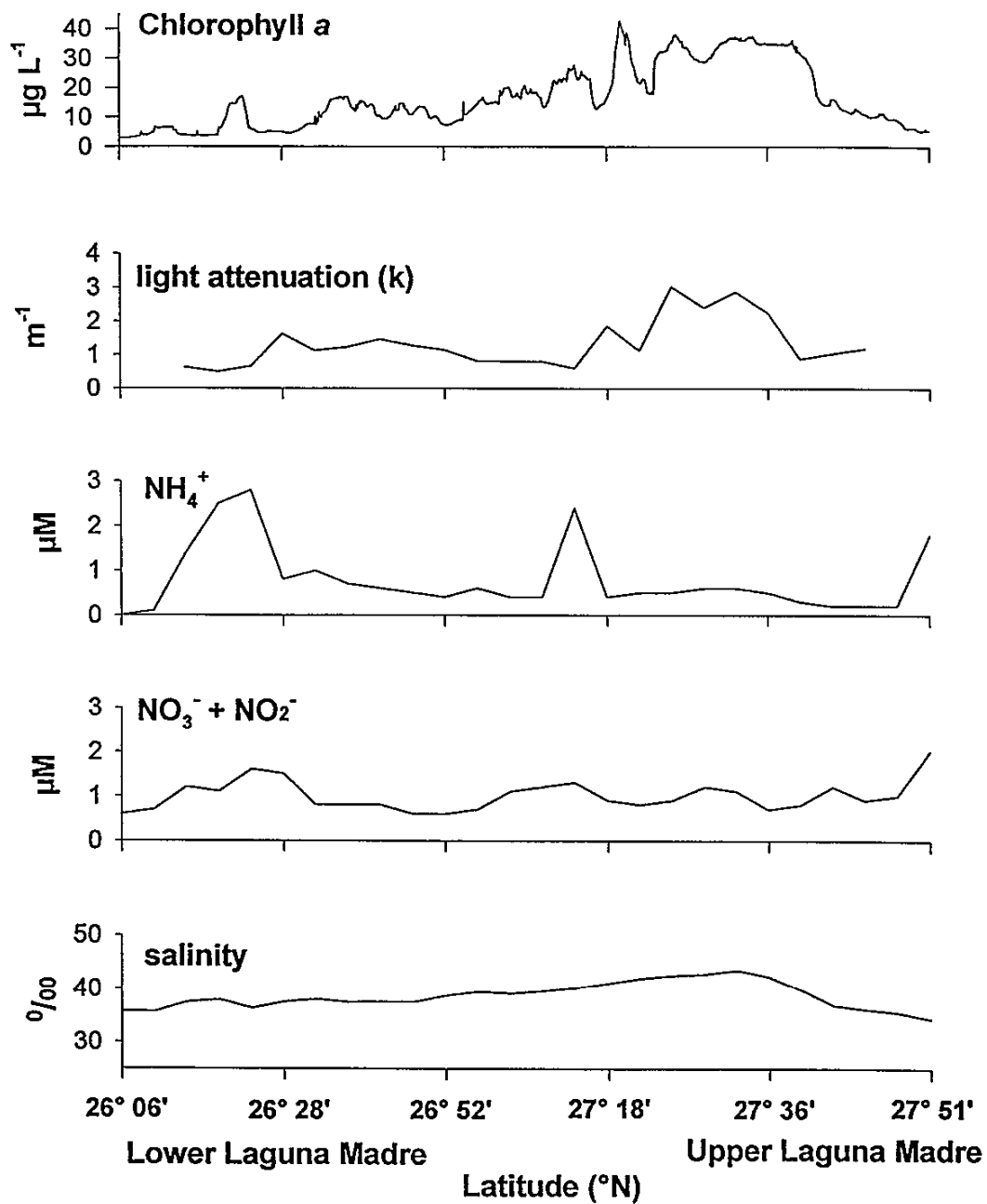


Figure 3. Variations in water column chlorophyll *a* with respect to other water column parameters measured along a transect from Corpus Christi Bay to Port Isabel, Texas on January 27, 1997.

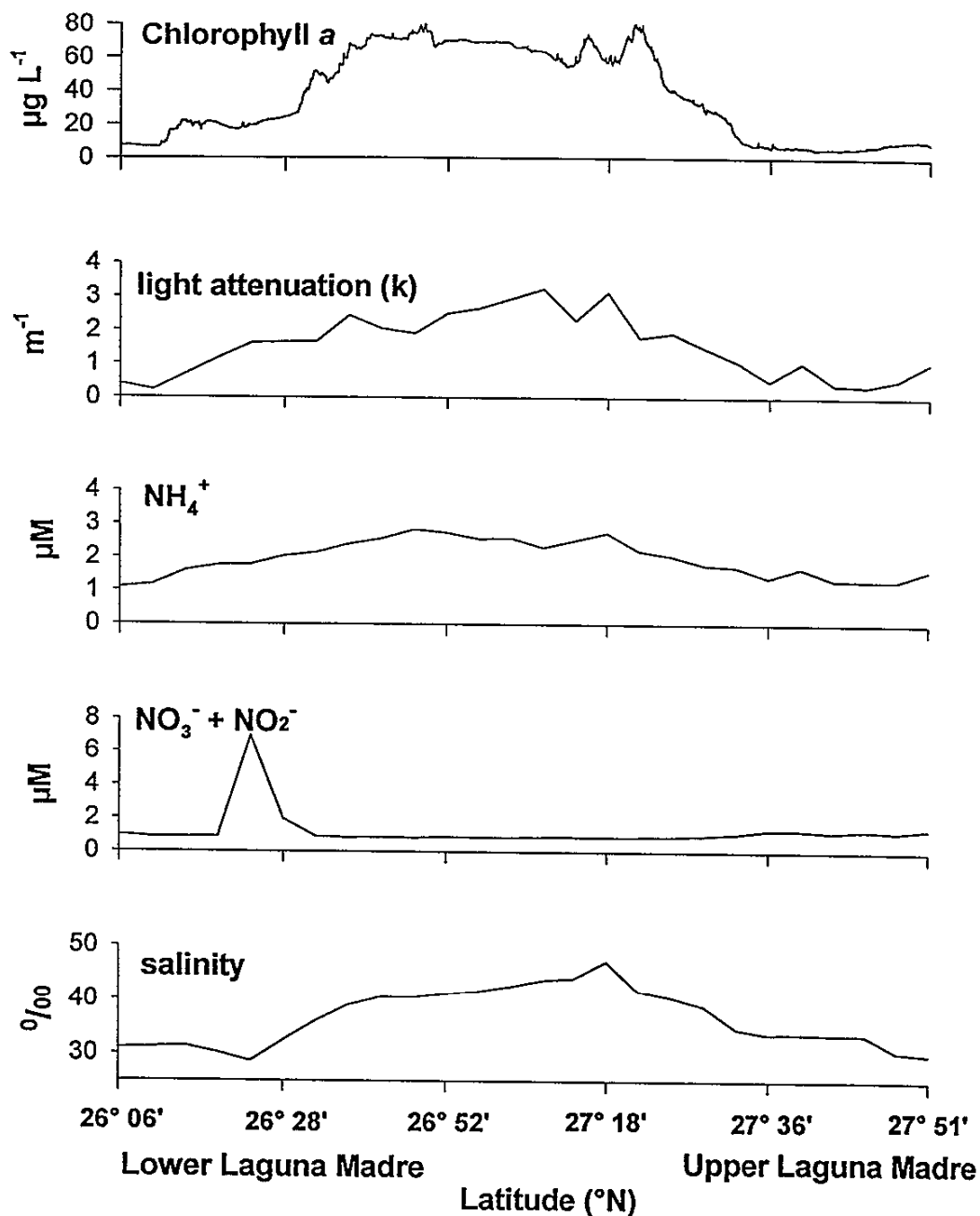


Figure 4 Seasonal changes in water column chlorophyll concentration in the upper Laguna Madre (ULM 1, 2, 3) and lower Laguna Madre (LLM 1, 2, 3) Values are mean \pm SE

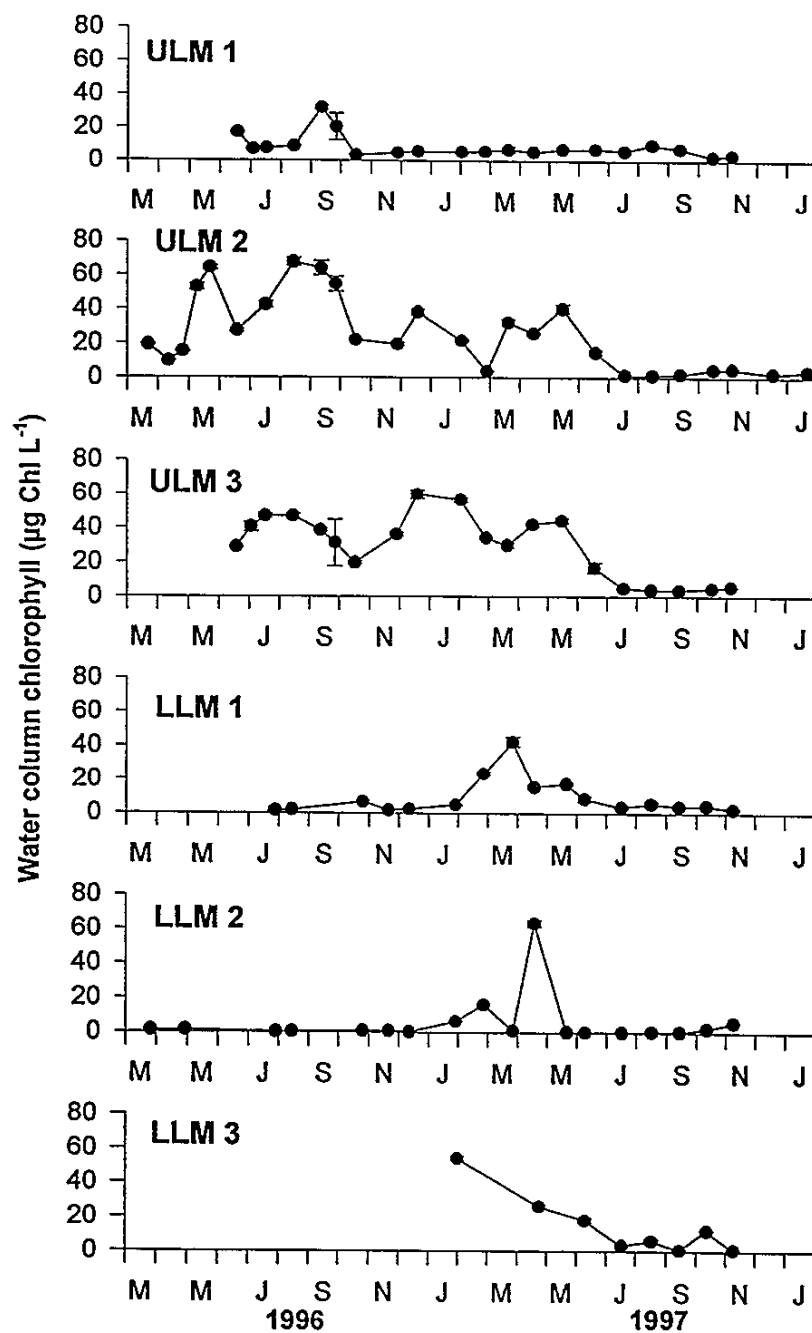


Figure 5. Variations in water column NH_4^+ concentration at the six permanent sampling stations in the Laguna Madre over the period of this study. Values are means \pm SE (n=4)

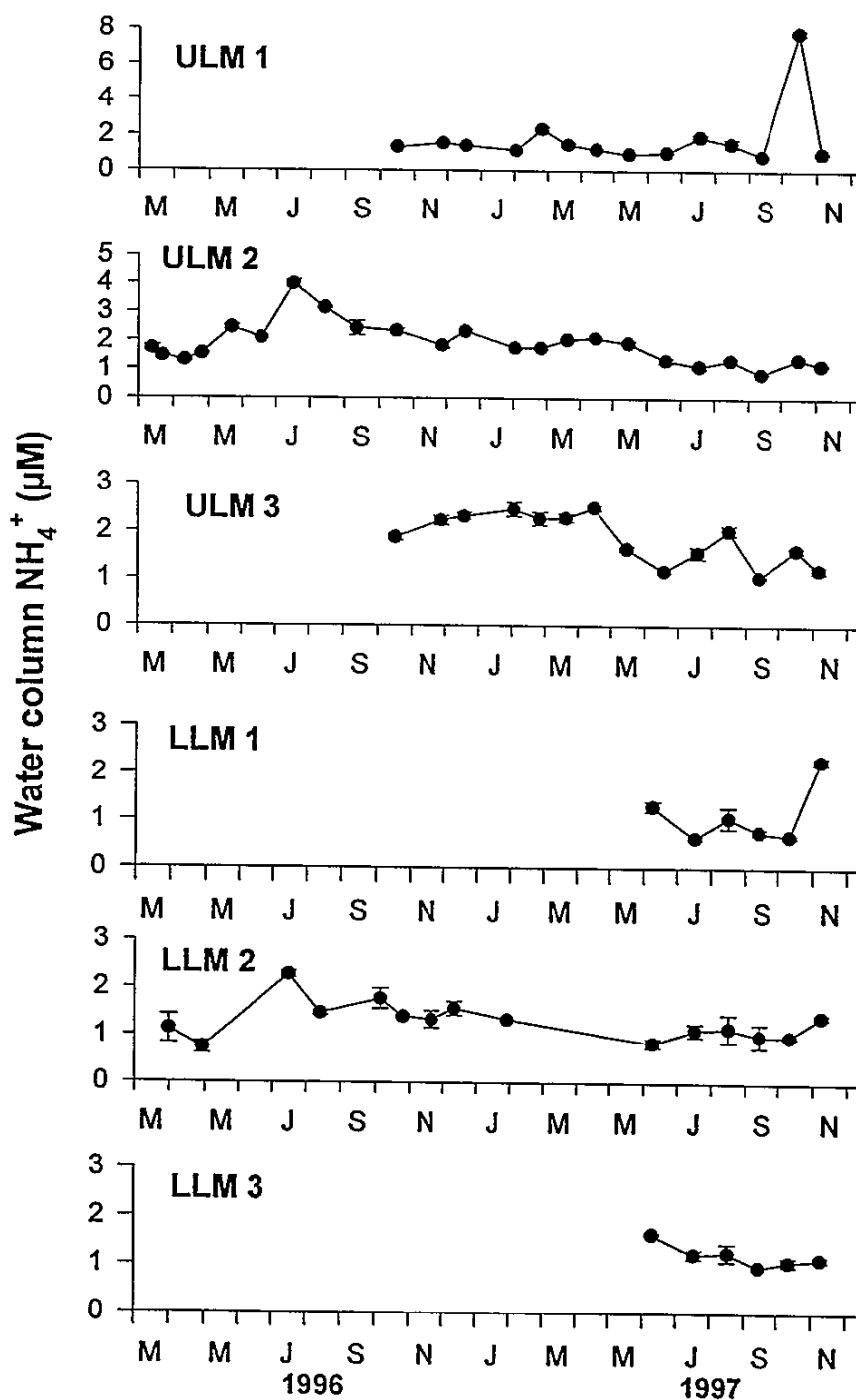
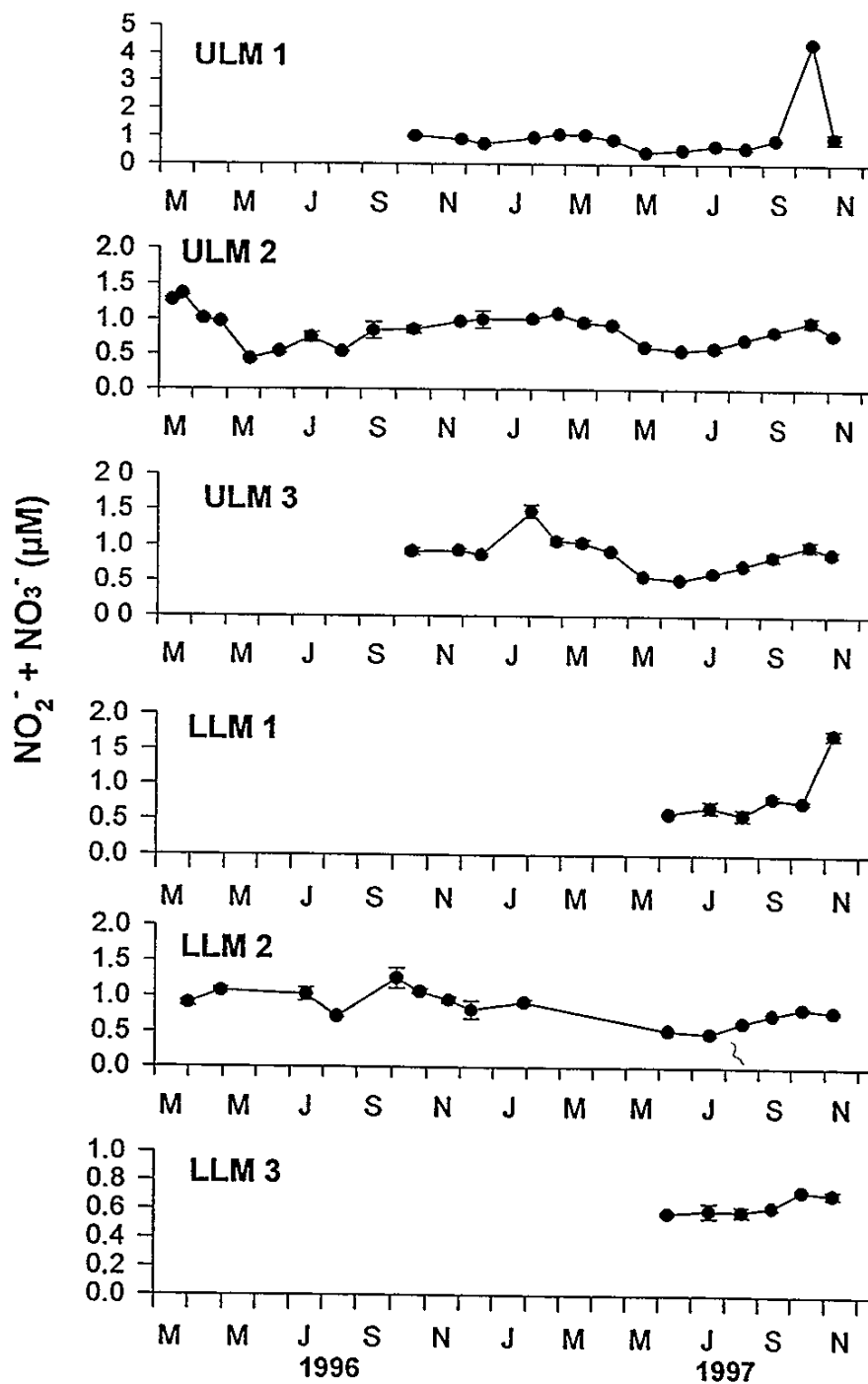


Figure 6 Variations in water column $\text{NO}_2^- + \text{NO}_3^-$ concentration at the six permanent sampling stations in the Laguna Madre over the period of this study. Values are means \pm SE (n=4).



Photon flux density

Surface irradiance (SI) exhibited a clear seasonal trend, lowest values were recorded in winter and highest in summer (*ca* 15 and 60 mol m⁻² d⁻¹, respectively). Continuous canopy-level measurements of PAR indicated that the underwater light environment was highly variable; daily values ranged from 0 to 35 mol m⁻² d⁻¹ for upper Laguna Madre (Fig. 7-9) and from 0 to 60 mol m⁻² d⁻¹ for lower Laguna Madre (Figs 10-12).

Diffuse attenuation coefficients (*k*) ranged from 0.1 m⁻¹ to as high as 10 m⁻¹ among the six permanent sampling stations. Average water transparency was greatest and *k* values lowest at ULM sites 1 and 2 and LLM site 2 (Table 3). The decline in the brown tide in ULM is clearly apparent after June 1997 at sites ULM 2 and 3. At ULM 3, *k* values over 7.0 m⁻¹ in January 1997 steadily declined to less than 2 by June. Light attenuation was clearly highest at LLM 1, with many values ranging between 4 and 10. The low transparency at this site clearly reflects the presence of unconsolidated sediments and dredged material deposits that are often resuspended by winds and waves--there are no seagrasses present at this site. In contrast, *k* values were generally <1.0 m⁻¹ for LLM 2 (Fig. 11) which is surrounded by dense grass beds. No underwater light data were collected at LLM 1 and 2 between February and June 1997. Missing underwater irradiance data at all sites in both 1996 and 1997 is related to rapid fouling of the underwater sensors, visits to the sites occurred every 12-14 days, but sensors were often visibly fouled after 10 days during the warmer months. Consequently, irradiance data was routinely removed from the data set after 10 days at sites where fouling was rapid (ULM 1, ULM 3, LLM 1, LLM 3).

Density and biomass

The density and above- and below-ground biomass of the three predominant seagrass species was measured at 12 stations throughout the upper and lower Laguna on a survey conducted in June 1996. *Thalassia* exhibited the lowest shoot density, ranging from 1,270 shoots m⁻² at site 30 to 1,950 shoots m⁻² at site 27 (Fig. 13). *Syringodium* and *Halodule* exhibited similar shoot densities, ranging from 2,200 to 6,800 shoots m⁻². In general, the highest shoot densities (for all species) were recorded for sites at the northern end of the sampling transect (Table 2, Fig. 13).

Figure 7. ULM 1 Daily integrated surface and underwater irradiance and light attenuation coefficients.

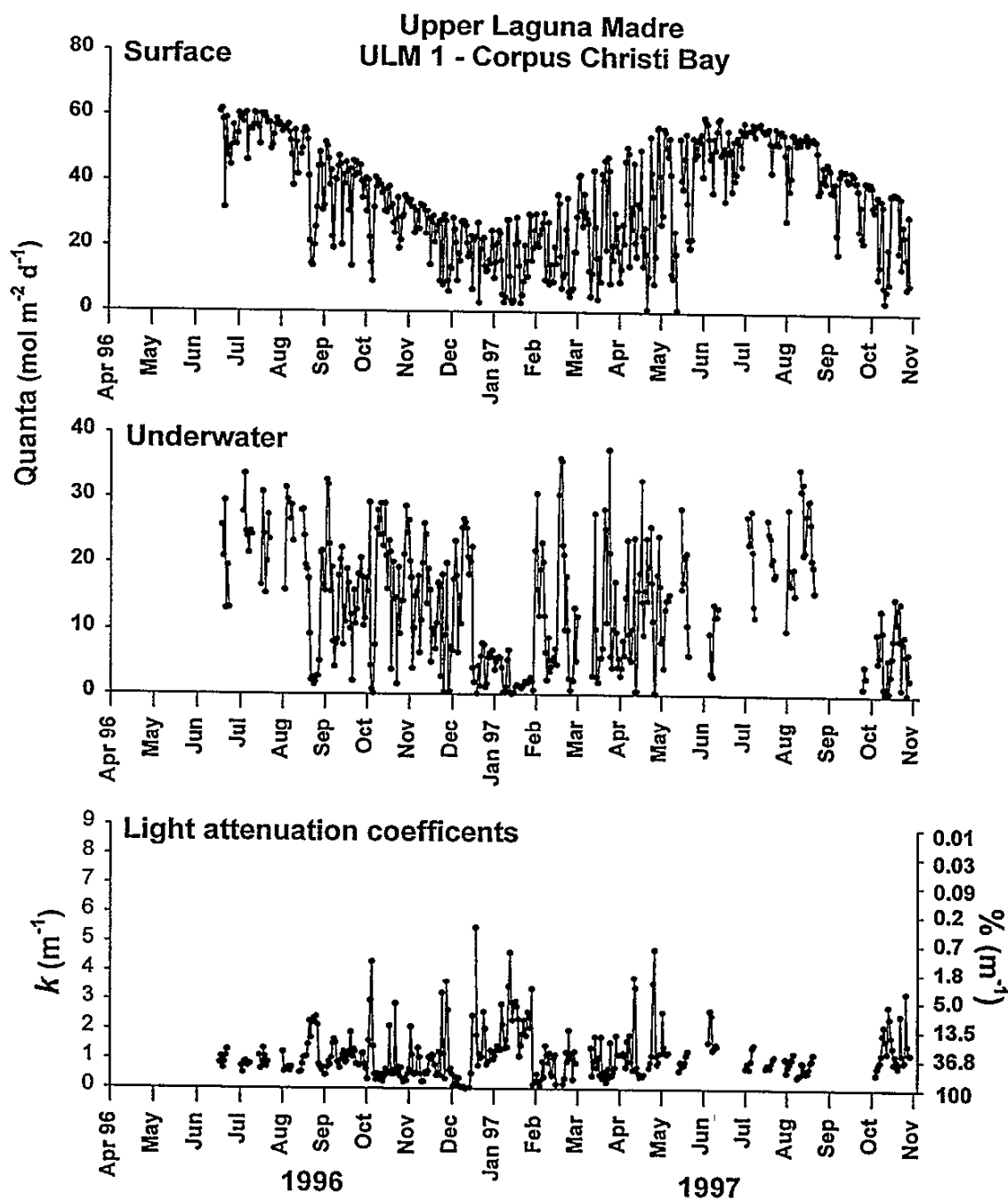


Figure 8 ULM 2 Daily integrated surface and underwater irradiance and light attenuation coefficients

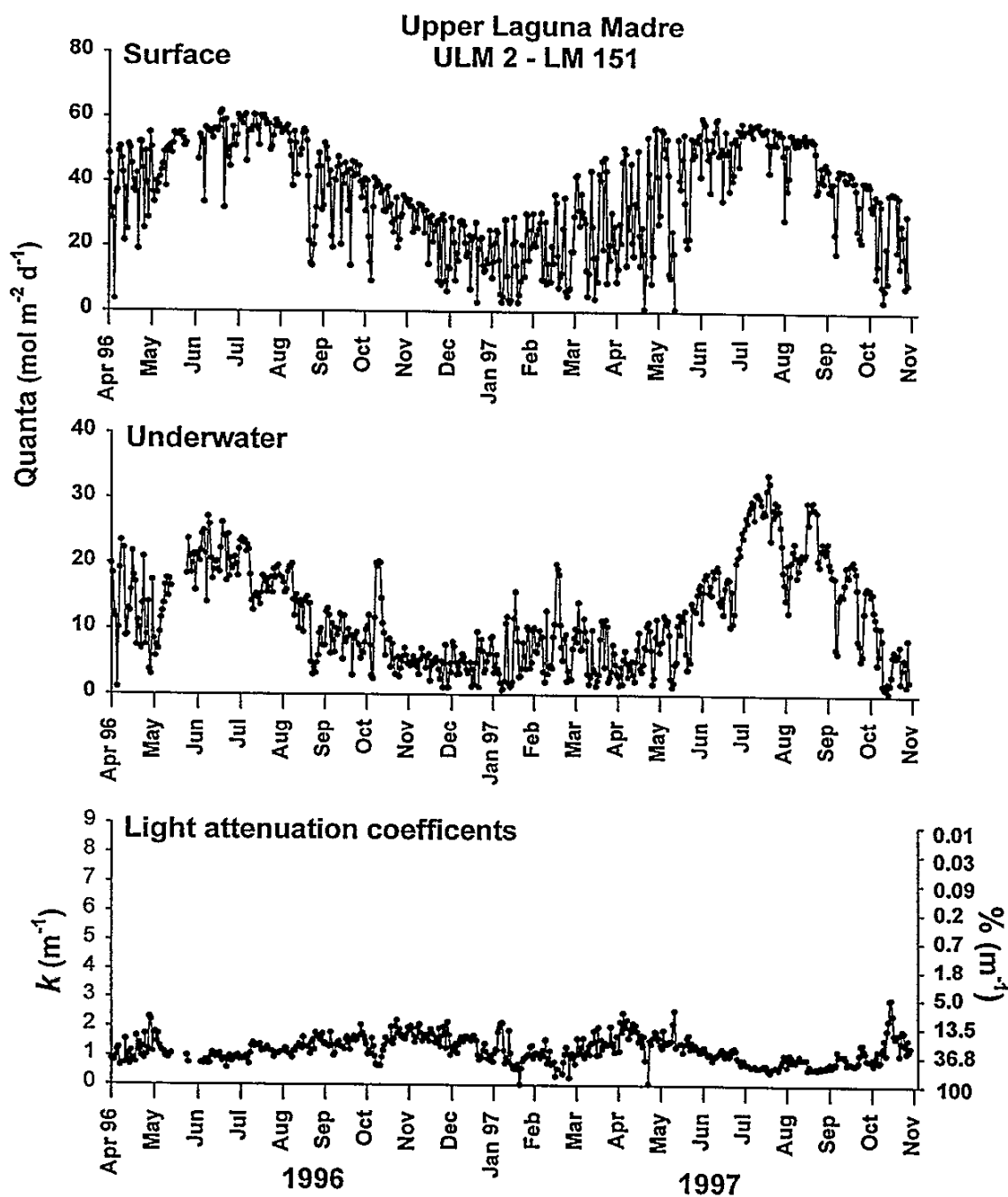


Figure 9. ULM 3. Daily integrated surface and underwater irradiance and light attenuation coefficients

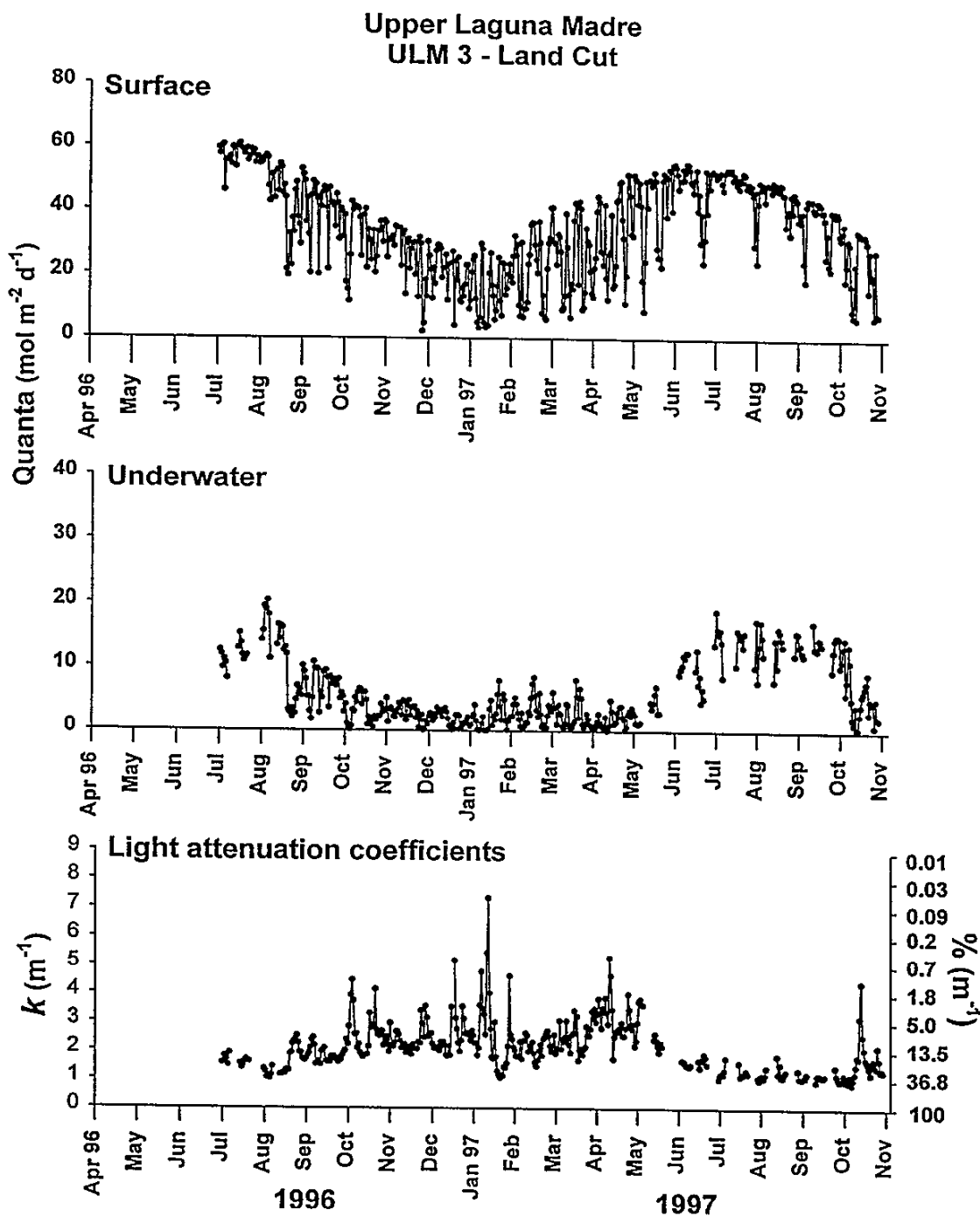


Figure 10 LLM 1 Daily integrated surface and underwater irradiance and light attenuation coefficients

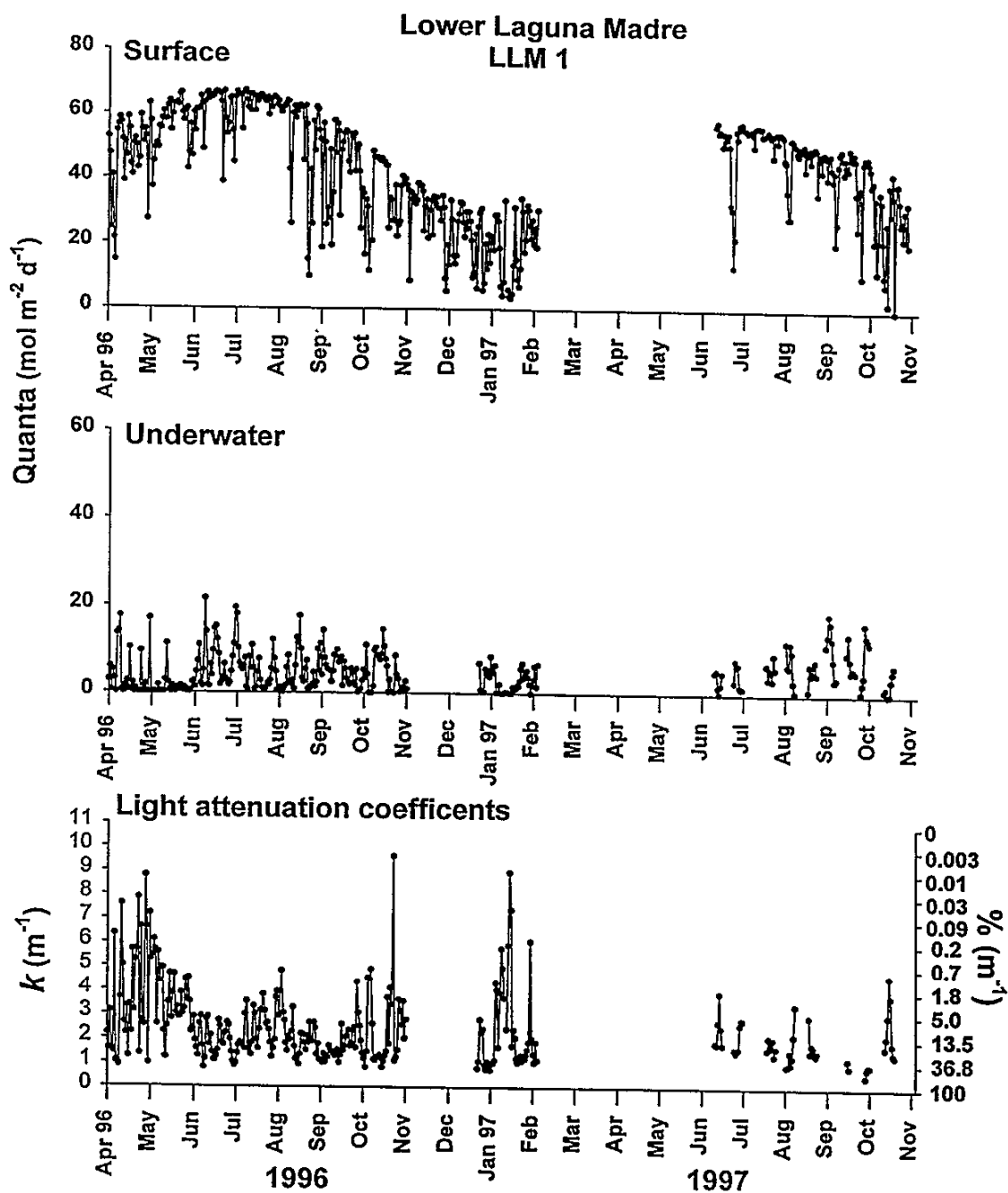


Figure 11 LLM 2 Daily integrated surface and underwater irradiance and light attenuation coefficients

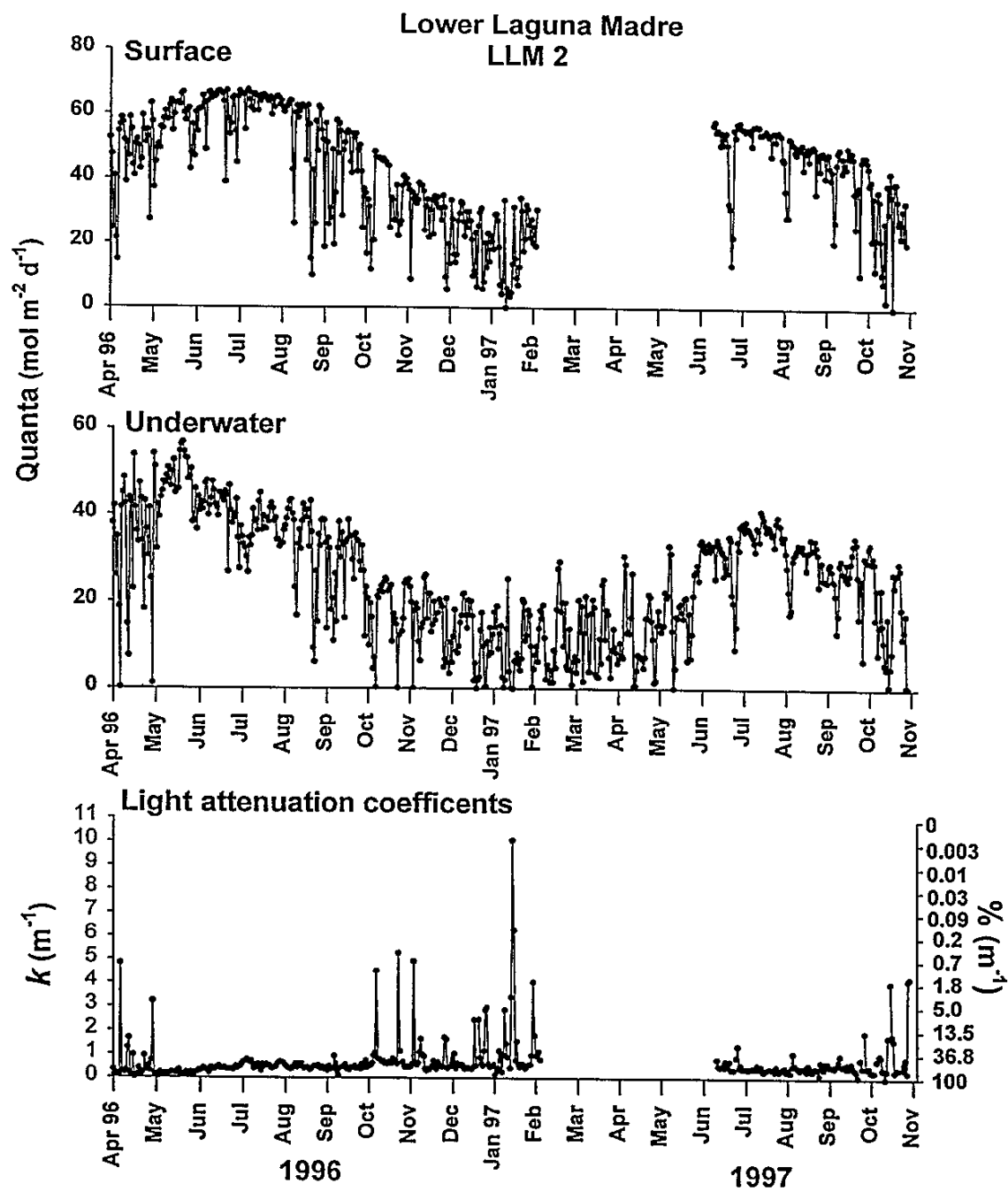


Figure 12. LLM 3. Daily integrated surface and underwater irradiance and light attenuation coefficients

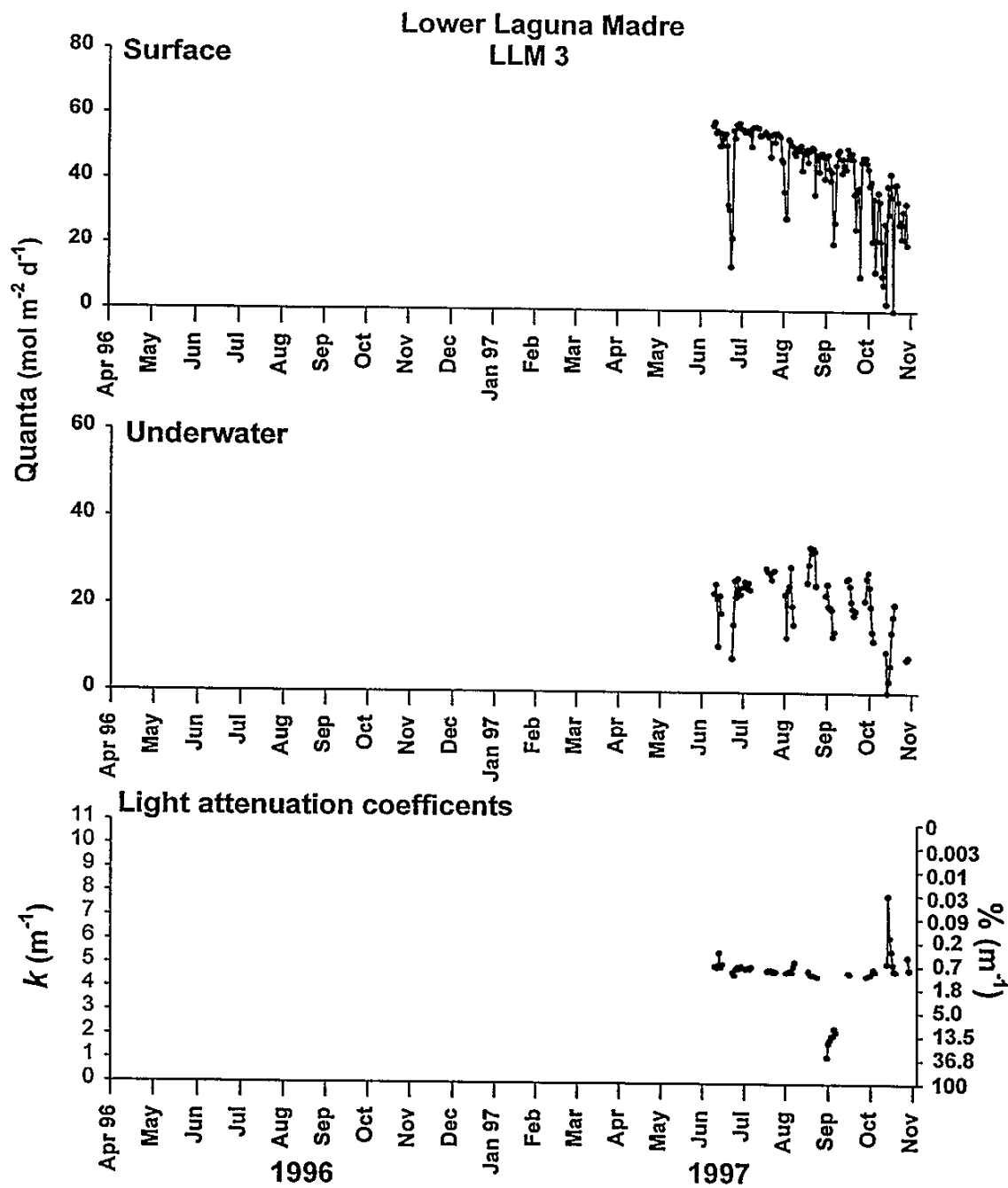


Figure 13. *Thalassia*, *Syringodium* and *Halodule* Shoot density, total biomass and root/shoot ratio for seagrass species along the Laguna Madre transect. Values represent means \pm SE (n=4).

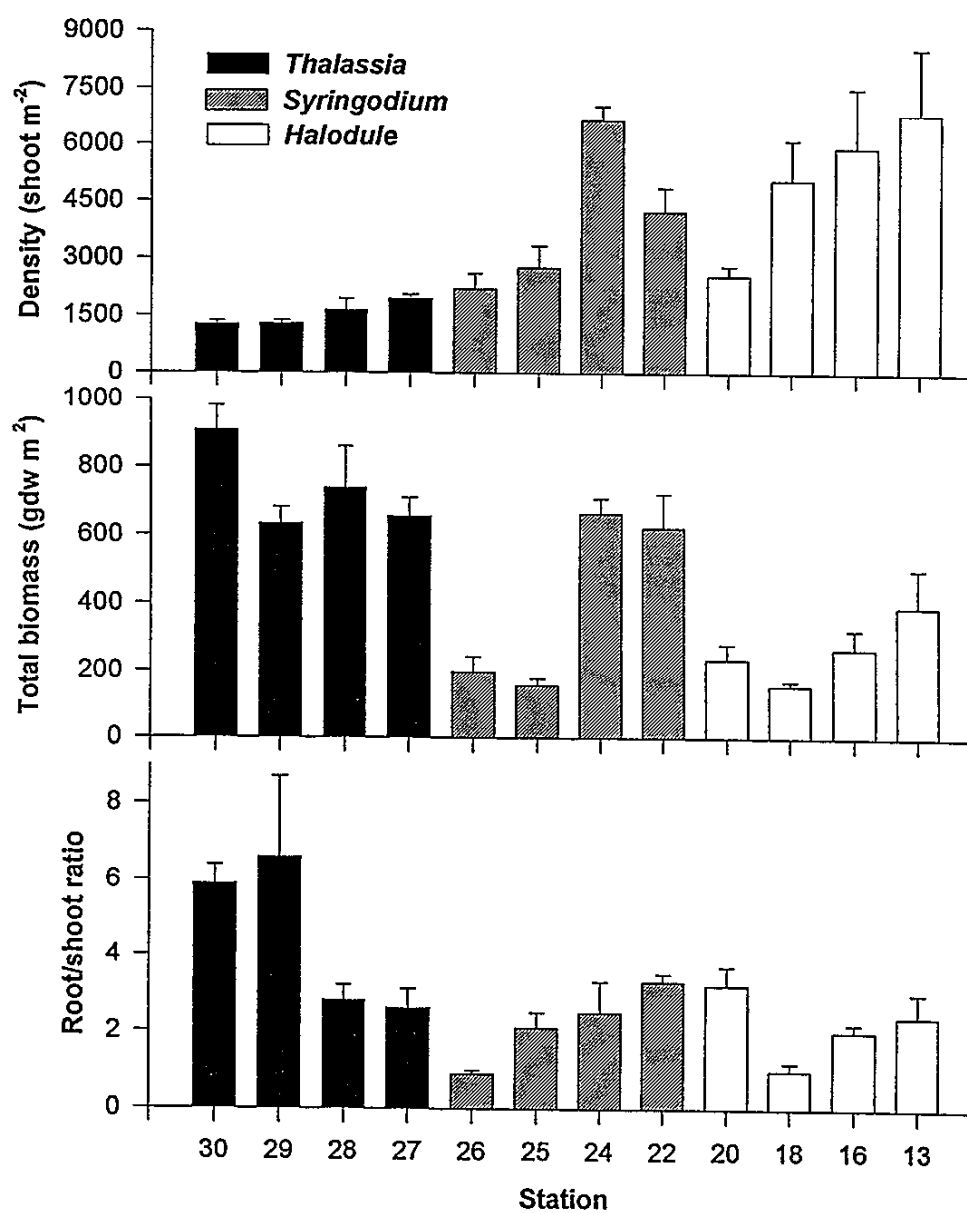


Table 3. Average surface irradiance (SI) and diffuse attenuation coefficients (k) characteristic of each of the permanent sampling stations based on total daily quanta received by surface and underwater sensors

Site	Number of Days N	Mean SI (SE) %	Mean k (SE) m^{-1}
ULM 1	350	40 (1.144)	1.148 (0.044)
ULM 2	553	32 (0.553)	1.220 (0.018)
ULM 3	388	16 (0.498)	2.128 (0.043)
LLM 1	305	10 (0.539)	2.451 (0.089)
LLM 2	442	59 (0.919)	0.702 (0.045)
LLM 3	35	15 (1.856)	1.766 (0.150)

In contrast, *Thalassia* was found to exhibit the highest biomass, which ranged from 630 to 900 $gdw\ m^{-2}$. There was no evident correlation between total biomass and shoot density for this species. Biomass of *Syringodium* was highly variable with sampling site, values ranged from 150 $gdw\ m^{-2}$ at site 25 to 670 $gdw\ m^{-2}$ at site 24. *Halodule* exhibited the lowest total biomass, which ranged from 150 to 390 $gdw\ m^{-2}$. *Thalassia* also had higher root/shoot ratios (2.6-6.6), while those of *Syringodium* and *Halodule* were similar (0.9-3.3) (Fig. 13).

Temporal changes in density and biomass in *Halodule*, *Syringodium*, and *Thalassia* were measured at sites ULM 2, LLM 3, and LLM 2 respectively, between June 1996 and May 1997 (Table 4). All three species showed distinct seasonal changes in density and biomass. Ratios of below-ground to above-ground biomass were clearly highest in winter (3-8), and lowest in summer (2-6), which largely reflect the major seasonal changes in the abundance of photosynthetic shoot and leaf tissues. Consistent with the station survey results (above), *Thalassia* exhibited the highest biomass (over 900 $gdw\ m^{-2}$), but highest shoot density was characteristic of *Halodule* (over 8,000 m^{-2}), with *Syringodium* intermediate between the two species.

Blade chlorophyll

Total blade chl content of *Halodule* (7.92-11.42 $mg\ chl\ gdw^{-1}$) was higher than that of either *Syringodium* (2.26-7.33 $mg\ chl\ gdw^{-1}$) or *Thalassia* (3.62-6.35 $mg\ chl\ gdw^{-1}$). However, chl $a:b$

Table 4 Density and biomass changes of three seagrass species, *Thalassia testudinum*, *Syringodium filiforme* and *Halodule wrightii*

	Sampling Date			
	June 1996	September 1996	January 1997	May 1997
<i>Thalassia testudinum</i>				
Density (shfts m ⁻²)	1273.5 ± 96.7	2165.0 ± 58.3	1471.6 ± 189.1	1316.0 ± 155.7
Biomass (gdw m ⁻²)	909.6 ± 72.3	642.3 ± 41.5	819.3 ± 136.5	993.9 ± 97.9
Root/shoot ratio	5.9 ± 0.5	3.6 ± 0.3	7.5 ± 0.5	6.2 ± 0.9
<i>Syringodium filiforme</i>				
Density (shfts m ⁻²)	6664.7 ± 384.1	2858.3 ± 668.3	2731.0 ± 810.2	3905.4 ± 585.9
Biomass (gdw m ⁻²)	665.5 ± 43.4	246.3 ± 59.9	231.1 ± 51.5	314.5 ± 58.8
Root/shoot ratio	2.5 ± 0.8	1.5 ± 0.1	3.5 ± 0.4	3.6 ± 0.6
<i>Halodule wrightii</i>				
Density (shfts m ⁻²)	5919.1 ± 1587.0	8192.9 ± 660.2	6480.7 ± 1094.0	8235.3 ± 1124.8
Biomass (gdw m ⁻²)	265.5 ± 55.6	365.4 ± 13.4	346.9 ± 41.7	522.5 ± 75.7
Root/shoot ratio	2.0 ± 0.2	2.0 ± 0.2	8.1 ± 0.9	3.4 ± 0.8

ratios from *Thalassia* leaf tissues (3.0-3.6) were higher than those from *Syringodium* and *Halodule* (2.2-2.7) (Fig. 14). There were no clear patterns in chl content between stations for each species, except for *Syringodium*, in which total chl was higher at stations 25 and 26 than at stations 22 and 24.

Carbon and nitrogen content

Carbon content in *Thalassia* leaf tissues showed seasonal variation, with highest values (37%) in late summer compared to less than 34% in winter; rhizome tissue carbon content ranged from a high of 37% in summer to 35% during the remainder of the year (Fig. 15). Leaf tissues had higher nitrogen content (>1.7%) than rhizome tissues (<1%) throughout the study period, exhibiting lowest (1.7%) levels in summer and highest (2.7%) in late winter. Nitrogen content of rhizome tissues showed little seasonal variation. Carbon:nitrogen (C:N) ratios ranged between

39 and 53 for rhizomes and 13 and 22 for leaves. The ratios for both tissues showed similar seasonal trends (Fig. 15).

Tissue nitrogen and carbon content exhibited distinct variations as a function of leaf age. Compared with young, newly formed tissue, both carbon and nitrogen content were lower and C:N ratio higher in older more senescent leaf parts (Table 5). Carbon content decreased from *ca* 38% to 34%, and nitrogen, from 2.1% to 1.1%

Discussion

Underwater light reduction has been linked to decreases in shoot density and biomass of seagrasses (Czerny and Dunton 1995, Lee and Dunton 1996). In estuarine systems, light penetration through the water column is regulated by concentrations of total suspended solids and chlorophyll. In the Laguna Madre, underwater light conditions may be predicted as a function of water column chlorophyll concentration, especially in ULM where the brown tide bloom persists. At several sites in ULM there was a strong correlation ($r^2 = 0.65$) between water column chl and k values, while there was a weak correlation ($r^2 = 0.14$) between TSS and k values (Dunton *et al* 1994). In general, we found that light attenuation in the ULM was highest during periods when chl concentrations were high. In LLM, winter fluctuation in k values (up to 5 m^{-1}) were more site specific, in that increases in k were related to either a short brown tide event (i.e. winter increases in water column chl resulted from the movement of brown tide from ULM via winter storm fronts; e.g. stations LLM 2 and 3) or to the re-suspension of sediments.

Table 5. Tissue carbon and nitrogen contents in different leaf parts of *Thalassia testudinum* collected from the lower Laguna Madre (LLM 2) in October 1997. Values are means \pm SE (n=3)

	Leaf part		
	Juvenile	Mature	Senescent
C (wt %)	37.83 \pm 2.09	37.81 \pm 2.16	33.76 \pm 2.49
N (wt %)	2.16 \pm 0.11	2.10 \pm 0.08	1.12 \pm 0.13
C/N ratio	20.41 \pm 0.19	20.98 \pm 0.51	35.48 \pm 2.07

Figure 14. *Thalassia*, *Syringodium* and *Halodule*. Total chlorophyll and chl *a* *b* ratios in seagrass leaf tissues. Values represent means \pm SE (n=6).

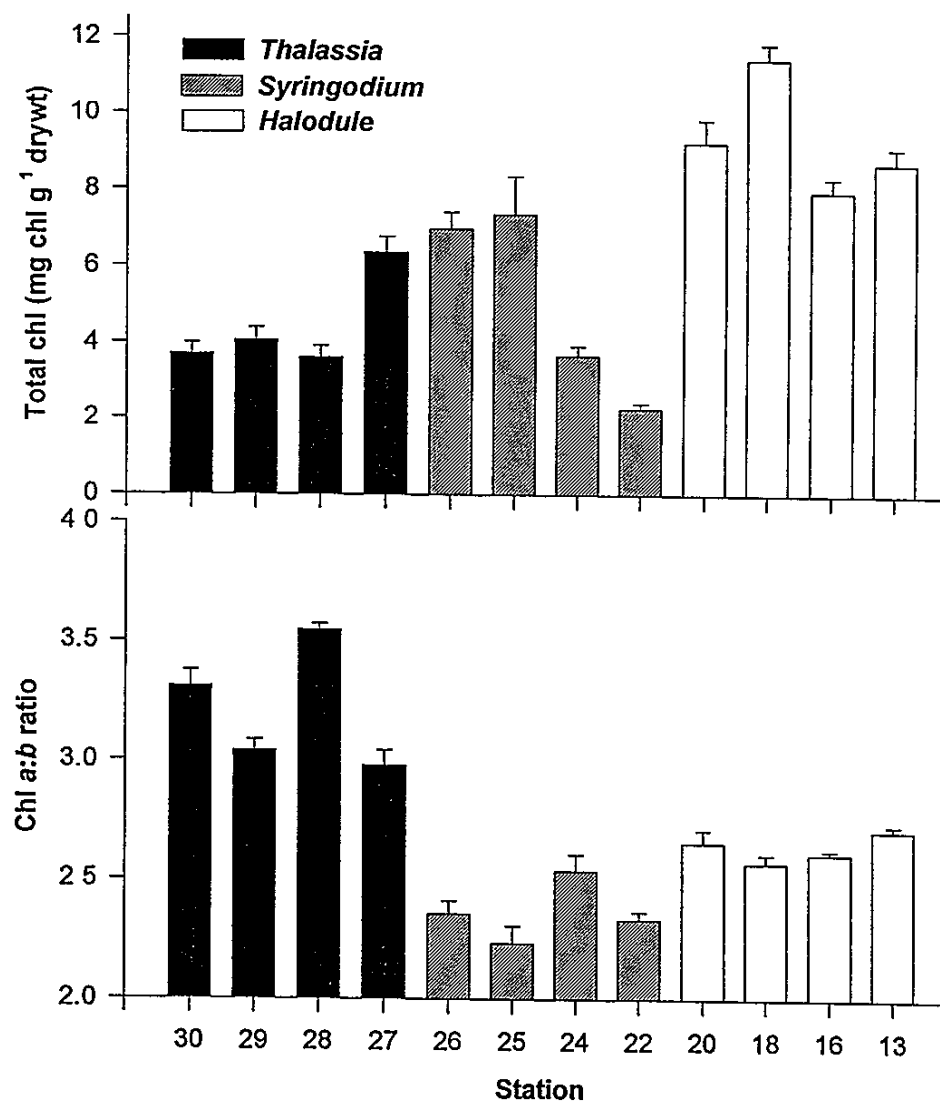
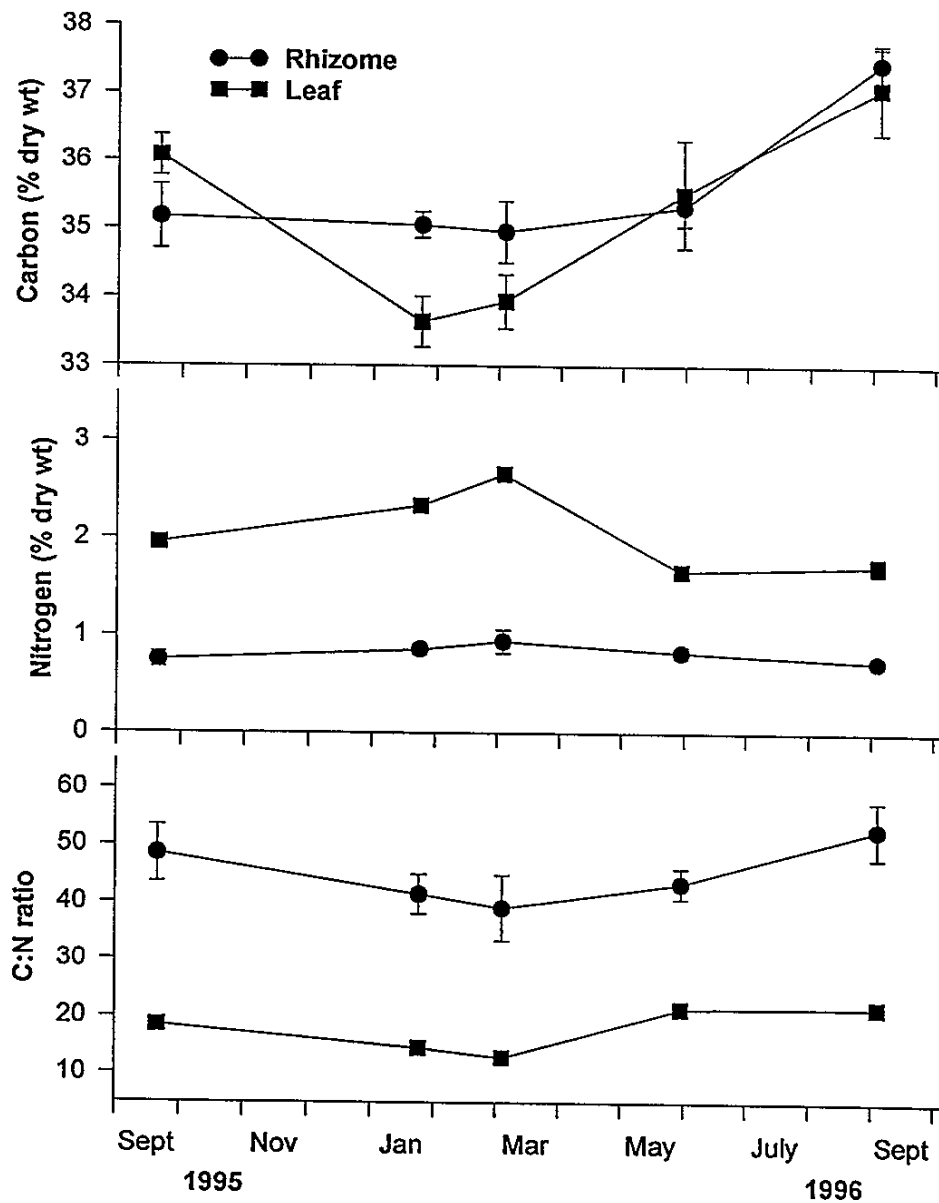


Figure 15. *Thalassia* Seasonal changes in carbon and nitrogen contents of leaf and rhizome tissues. Values represent means \pm SE (n=4). Where no error bars appear, SE is less than the size of the symbol



(LLM 1) Seagrass density and biomass did not exhibit pronounced negative correlations relative to water column chlorophyll. We suggest that the short-term winter appearance of brown tide in LLM does not impact seagrasses, since photosynthesis and respiration are already reduced by low water temperatures.

A pronounced spatial variation in water column chlorophyll concentration was directly correlated with the distribution of brown tide algae along the Laguna Madre transect. Although chl values exhibit seasonal variation, the lowest values from ULM were nearly two-fold higher than those from LLM. In general, ULM has much higher chl concentrations (almost 80 mg L⁻¹) and much lower underwater irradiance levels. The loss of seagrass stands from deeper portions of the ULM (Onuf 1996) have been directly attributed to a 50% reduction in underwater light caused by the brown tide (Dunton 1994)

Seagrass biomass and density patterns were similar to previously published reports (Dunton 1994, Czerny and Dunton 1995, Lee and Dunton 1996). Species-specific differences in biomass were expected, since these plants exhibit marked morphological differences. *Thalassia* has large, flat blades and a prominent rhizome system, while *Halodule* has very fine blades and rhizomes. *Syringodium* has round leaves and is intermediate in size by comparison. Large root:shoot ratios may be explained by the fact that approximately 80% of seagrass biomass is typically below ground. Patterns for carbon, nitrogen and C:N ratios were similar to those reported by Lee and Dunton (1996).

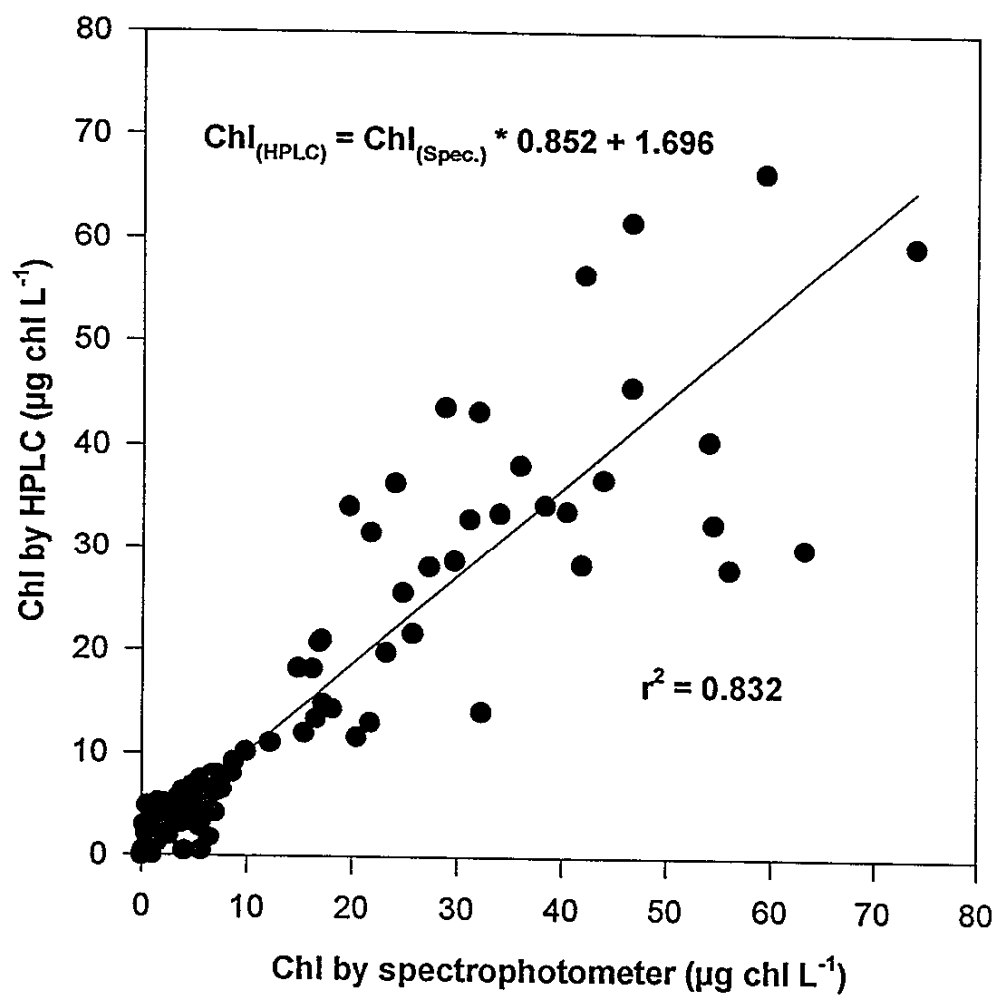
Some seagrass genera (e.g., *Zostera* and *Thalassia*) exhibit the ability to photoacclimate in response to changes in light availability by adjusting pigment content and stoichiometry (Wiginton and McMillan 1979, Dennison and Alberte 1982, 1985, Abal et al. 1994, Lee and Dunton 1996). However, the purpose of this research was to collect background information on the pigment levels of three grass species from a variety of locations. Previous work has demonstrated that *Halodule*, unlike *Thalassia*, does not exhibit a “classic” photoacclimation response (Dunton, 1994, Lee and Dunton, 1996) as previously reported for higher plants

(reviewed by Boardman 1977, Bjorkman 1981). Therefore, as indicated by the data, no distinct variations in *Halodule* pigment content were noted. *Halodule* was observed to be the dominant species and exhibited the highest total chlorophyll content. *Halodule wrightii* can be classified as an “opportunistic” species (Czerny and Dunton 1995), and the maintenance of high chlorophyll levels may contribute, in part, to this plant’s ability to tolerate environmental disturbance (i.e. reductions in light quality/availability).

High salinity values obtained in ULM were probably related to a very limited water exchange between this area and the Gulf of Mexico. Although both ULM and LLM are hypersaline, the water exchange in LLM is higher due to the proximity of the Mansfield and Brazos-Santiago Passes. Overall, nutrient levels were low. Water column ammonium exhibited two peaks, one near the mouth of Baffin Bay and again near the mouth of the Arroyo Colorado. These peak ammonium values may have resulted from agricultural run-off and/or municipal effluent into the Laguna Madre system.

Water column chlorophyll concentrations were estimated by traditional spectrophotometric (this chapter) and high performance liquid chromatography (HPLC) methods (Chapter 5). Comparison between these two techniques yielded an excellent correlation (0.832), but despite the positive correlation, chl values determined by the spectrophotometric technique consistently underestimated chl content on the same water sample (Fig. 16). Additionally, HPLC appears to be more sensitive for detecting very low levels of chlorophyll, while at high pigment concentrations (i.e., similar to those noted in ULM) traditional methods may be more sensitive.

Figure 16 Correlation between water column chlorophyll estimates derived from traditional spectrophotometric and high performance liquid chromatography (HPLC) methods.



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